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VOLUME 15 SEPTEMBER, 1941 NUMBER 5

TRIAS AT NEW PASS, NEVADA (NEW LOWER KARNIC AMMONOIDS)

FRANCIS NEWLANDS JOHNSTON
Chevy Chase, Md.

ABSTRACT—In studying the Triassic limestone beds of the Star Peak group exposed in a homoclinal section in South Canyon, New Pass or Desatoya Range, Nevada, an ammonite zone hitherto unknown in North America was discovered. This is called the *Joannites* zone and is approximately the equivalent of the zone of *Trachyceras aon* or of *Trachyceras anonoides* in the Alpine section typical for the marine Trias. The lithological and faunal sequence is summarized, and ammonites of the following genera are described: *Clionites, Hannaoceras, Lecanites, Arpadites* s.s., *Perrinoceras* n.g., *Metahedenstroemia?, Sageceras, Lobites* s.s. and *Lobites* (*Coroceras*), *Arcestes* (*Proarcestes*) and *Arcestes* (*Anisarcestes?*), *Joannites, Paracladiscites, Procladiscites,* and *Trachyceras* s.s.

THE NEW PASS RANGE lies in central Nevada about 25 miles in a straight line west of Austin and along the boundary line between Lander and Churchill Counties. It is that part of the Desatoya Mountains north of the New Pass. The most detailed map of the area to date is Map V, "Nevada Basin," in the Atlas of the Fortieth Parallel Survey, 1876. The range also appears on the U. S. Land Office map of Nevada, 1930 edition.

The author first went to New Pass at the suggestion of the late Dr. James Perrin Smith of Stanford University. A Master's thesis, completed under the direction of Dr. Smith in 1930, described some of the genera from the *Joannites* zone published herewith. The work was continued after some years' interval at the Catholic University of America under the direction of Dr. Arthur R. Barwick. Study was carried on in the United States National Museum through the courtesy of Dr. R. S. Bassler of the museum and of Dr. J. B. Reeside of the United States Geological Survey.

The general stratigraphy of the region has been described in the reports of the Fortieth Parallel Survey by S. F. Emmons (1877, vol. 2, pp. 644–649) and Clarence King (1878, vol. 1, pp. 282–284, 630–632). The highest part of the range is composed of siliceous rocks—especially of a conglomerate of siliceous pebbles in a siliceous matrix—overlain on the west and southwest by a band of limestone extending for about 6 miles along the range front and intruded on the south by a "diorite" body about which are grouped the gold-quartz veins worked at the New Pass Mines. The limestone is overlain by or faulted against rhyolite except when in contact with outwash alluvium. The siliceous beds are assigned to the Koipato group, and the calcareous beds (limestones) to the Star Peak group.

Intensive study was made of the limestones because they are fossiliferous and yield abundant remains of ammonites and of other organisms at certain horizons. There are no fossils known from the other rocks of this region. The fossils from the

limestones have been described or referred to by Leidy, Gabb, Meek, Merriam, J. P. Smith, and Muller. Other references to this limestone are found in Raymond (1869, p. 76–77), White (1869, p. 87), and Lincoln (1923, p. 114).

Fossils of Middle Triassic age were early recognized in the limestone at New Pass. There are abundant ammonites, although pelecypods and remains of vertebrates are not lacking. These are similar to the Middle Triassic fauna from the West Humboldt Range. They can be found fairly regularly all along the range front, within a stratigraphic distance of about 500 feet above the contact, here conformable, with the siliceous Koipato beds. Locally sliding seems to have taken place along the contact.

Muller (1936, p. 206) mentions corals in South Canyon between the zones of *Ceratites trinodosus* (Middle Trias) and *Trachyceras aon* (Upper Trias). Their age might be Ladinic (top of the Middle Trias).

In South Canyon is exposed the best section of the limestone found anywhere along the range front. Along both sides of this canyon cephalopods of the zone of *Trachyceras aon* were found, but they were not found elsewhere along this range front. A summary of the section as exposed in South Canyon follows:

1. Koipato formation. Permian? (Wheeler, 1939). Over 3000 feet of siliceous, noncalcareous beds comprise this formation. Along the crest of the range it consists of massive reddish poorly sorted conglomerate. Near the conformable contact with the overlying limestones it is a brown schistose fine-grained rock veined with calcite and quartz.
2. Star Peak formation. Triassic. About 2900 feet thick. Consists principally of limestone.

   a. Acrochordiceras zone. Lower Anisic. This consists of about 300 feet of thin-bedded limestones and calcareous shales conformably overlying the siliceous Koipato beds and grading upwards into the *Daonella* zone, from which it is separated on the basis of fossils. In this zone occur such ammonite genera as *Acrochordisceras, Cuccoceras, Balatonites, Monophyllites, Dalmatites* (or *Longobardites?*), and *Haydenites;* along with the pelecypods *Sphaera whitneyi, Modiomorpha lata, M. ovata,* and *Posidonia,* some nautiloids, and vertebrate remains. Probably *Cymbospondylus piscosus* Leidy came from the bottom of this zone.

   b. Daonella zone, equivalent to the zone of *Ceratites trinodosus.* Upper Anisic. About 300 feet of calcareous shales becoming more massive above and mottled with red noncalcareous blotches. The lower 150 feet of shales contain the ammonites *Paraceratites, Gymnotoceras,* and other *Ceratites, Eutomoceras,* etc.; the nautiloids *Paranautilus multicameratus* Gabb, *Germanonautilus furlongi* Smith, and *Orthoceras;* the characteristic pelecypod *Daonella;* and some vertebrae presumably saurian.

   c. Coral zone. Ladinic (or Karnic?). The lower 200–250 feet have lenticular layers of gritty and conglomeratic limestone (siliceous pebbles in a matrix of gray limestone) and beds of sandstone. The upper 750 feet are chiefly massive limestones alternating with thinner layers and shales. The corals mentioned by Muller occur about 500 feet below the top. There are fossils—chiefly pelecypods, gastropods, and crinoid stems—which are not well preserved.

   d. Joannites zone (or zone of *Trachyceras aon*). Bottom of the Karnic. This consists of about 500 feet of thin-bedded limestones and calcareous shales. At the base are one or more limestone beds about 6 inches thick, which are practically a coquina of brachiopods. *Rhynchonella alteplecta* (Böckh) Smith occurs in this layer, also Spiriferinas and terebratuloids. All the ammonites described below came from above the brachiopod layer. In addition are found *Orthoceras,* perhaps *Atractites,* a belemnite; numerous pelecypods of the genus *Halobia* and Aviculopectens. Perhaps *Lima* (*Limatula*) *erecta* Meek, described from the "Jurassic" (sic) of New Pass, belongs here. There are vertebrae 6 inches in diameter, also ribs.

   e. Red Rock limestone[1] Karnic? 800 feet of massive limestone forming the cliffs at the foot of South Canyon. It is badly jointed, fractured, and veined with calcite. Though not unfossiliferous, it yields no good specimens. The fossils are apparently gastropods, pelecypods, brachiopods, and crinoid stems.
3. Rhyolite. Tertiary. The rhyolite is reddish when weathered, gray on a fresh surface. It usually shows phenocrysts about ⅛ inch long of glassy quartz and of a white, opaque feldspar. The contact with the limestone at the foot of the South Canyon seems to be a fault on account of its straightness and the absence of outliers of rhyolite on the limestone. Elsewhere (to the south of this canyon) it seems depositional. Some rhyolite was noted with inclusions of limestone.

All but one of the ammonoids described or figured hereafter came from the *Joannites* zone, South Canyon, New Pass or Desatoya Range, Nevada.

The only ammonoid figured here that is not from New Pass is U. S. Nat. Mus. No.

[1] So called because it is believed to be equivalent to the "Red Rocks" at the head of Congress Canyon, West Humboldt Range, mentioned by Cameron (1939, p. 582).

3181 from Aussee, Austria. It is a *Trachyceras*, which is illustrated for comparison.

All measurements are in the metric system. Here follow some abbreviations used: D = maximum diameter; H = maximum height; H′ = maximum height from the venter of the inner whorl to the venter of the next outer whorl; W = maximum width; U = maximum width of the umbilicus;

Figures are natural size unless otherwise noted. All originals are in the United States National Museum. One National Museum number covers all specimens of a species from the same horizon and locality.

SYSTEMATIC DESCRIPTIONS

Genus CLIONITES Mojsisovics

"Gruppe der *Arpadites angulosi*" (*Clionites*) MOJSISOVICS. *1893*, pp. 450, 451.
Clionites HYATT and SMITH, *1905*, p. 181.
Clionites KITTL, *1908*, p. 490.
"Ueber *Clionites* und *Protrachyceras*" ARTHABER, *1914*, p. 134.
Clionites Smith, *1927*, p. 83.

Type: *Clionites angulosus* Mojsisovics (1893, p. 465, pl. 123, fig. 10).

The following subgenera are recognized:

Clionites s.s. Mojsisovics, Ladinic?, Karnic, and Noric of the Alpine-Mediterranean, Himalayan, East-Pacific, and Arctic regions.

Neanites Hyatt and Smith, Karnic of California.

Shastites Hyatt and Smith, Karnic of California.

Stantonites Hyatt and Smith, Karnic of California.

Traskites Hyatt and Smith, Karnic of California.

Californites Hyatt and Smith, Karnic of California.

Dawsonites J. Boehm, Karnic of British Columbia and of Bear Island.

In the strict sense *Clionites* includes evolute, discoidal, ribbed forms with low whorls increasing slowly in height. A ventral furrow is bordered by the ends of the ribs or by knots on the ends of these ribs. Marginal and umbilical knots may also be present, as well as lateral knots. The latter feature makes them resemble *Protrachyceras*, while a tendency towards fusion of the ventral knots make them resemble *Arpadites*, s.s. with two crenulated keels bordering the ventral furrow. Sutures are ceratitic.

For this last reason, probably, J. P. Smith has included his California species in this genus in the broad sense. The rough and spiny ornamentation of these species, however, makes them look more like some of the forms of *Trachyceras* from the Hallstatt limestone in spite of the fact the latter have ammonitic sutures. *Clionites* (*Traskites*) *robustus* Hyatt and Smith resembles as closely *Trachyceras hylactor* Dittmar (Mojsisovics, 1893, p. 645, pl. 173, fig. 1, 2) or *Trachyceras böhmi* Mojsisovics (1893, p. 647, pl. 173, figs. 4a, b) as it does *Clionites ares* Mojsisovics (1893, p. 478, pl. 144, fig. 2). Also compare *Trachyceras duplex* Mojsisovics (1893, pl. 180, figs. 4–6). The sutures shown in figure 6, are however, ammonitic and not ceratitic as on the California forms.

The forms from New Pass, Nevada, described below resemble much more closely *Clionites angulosus* Mojsisovics, the type of the genus, than they do Smith's California "*Clionites*." No lateral knots or spines are present. Sutures are ceratitic.

It might here be noted that the following species of Mojsisovics, with five spirals of knots, are all Noric, i.e., at a higher horizon than *Clionites* with three or fewer spirals of knots (such as the type *C. angulosus*, from the beds with *Trachyceras aonoides* of the Raschberg near Goisern, Austria): *C. ares* from the Someraukogel near Hallstatt, Austria; and *C. spinosus*, *C. hughesi* and related species, *C. salteri*, and *C. woodwardi* and variety *crassa*, all from the *Halorites* limestone of the Bambanag section in the Himalayas.

CLIONITES WHEELERI

Johnston, n. sp.
Plate 58, figures 1–8

	D	H/D	W/D	U/D	H/W	R[1]
(1)	28	0.33	0.26	0.42	1.24	37
(2)	20	0.32	0.28	0.39	1.23	27
(3)	13	0.41	0.38	0.29	1.08	32
(4)	35	0.30	0.29	0.46	1.05	33

[1] R = ribs per whorl.
(1–3) *C. wheeleri*, n. sp., pl. 58, figs. 6–8(1), figs. 4, 5(2), figs. 1–3(3).
(4) *C. torquati* Mojsisovics, 1893, p. 468, pl. 123, figs. 9a–c.

Number of specimens studied, four. These are discoidal, evolute forms ornamented with unforked, almost straight, radial ribs that stop in the middle of the venter, giving the impression of a ventral furrow. This is not a true furrow, however, as it does not sink below the level of the spaces between the ribs. The whorls are higher than wide, oval in cross section, embracing one-third of the preceding whorl, increasing slowly in height (about 150 per cent per revolution). The umbilical and ventral shoulders are gently rounded.

The ribs seem to be lacking on the extreme innermost whorls. The smallest specimen shows about 32 fine, straight ribs, which end abruptly on the venter, leaving the above-mentioned furrow between them. The ribs on the right half are opposite those on the left half. Intercostal spaces are no wider than the ribs. The ribs at first coarsen with increasing diameter, their ends become more projecting. At, however, about 20 mm. D they become finer, the ends do not project as heretofore, and the whole ventral part of the rib curves gently forward. On the largest specimen there is a tendency for one rib at the umbilicus to give rise to two on the flanks, but these again unite on the ventral shoulder to form one rib. At this point the ends of the ribs do not project at all, so that the ventral furrow is absent.

The sutures are unknown. The living chamber is at least one half revolution long.

This species resembles the general type of *Clionites angulosus* Mojsisovics which is the type species of the genus, with whorls higher than wide and without true knots or spines on the ribs. *C. torquati* Mojsisovics (1893, p. 463, pl. 123, figs. 9a–c) resembles fairly closely *C. wheeleri*, but the inner whorls grow in height less rapidly, ribs are not so fine at maturity and are forked in immaturity, the ventral furrow is always present, and the ribs are said to alternate on opposite sides of the venter (although this is not evident in pl. 123, fig. 9b). Sutures of *C. torquati* (fig. 9c) are ceratitic, with a ventral lobe divided into two points by a median saddle, a first lateral lobe largest of all, a smaller second lateral, and a tiny lobe next to the umbilical suture. Mojsisovics had one specimen, from the beds with *Lobites ellipticus* of the Feuerkogel on the Röthelstein near Aussee, Austria.

The species is named in honor of Dr. Harry Edgar Wheeler of the University of Nevada.

CLIONITES BARWICKI

Johnston, n. sp.

Plate 58, figures 9–18; text figure 1A

	D	H/D	W/D	U/D	H/W	K[1]
(1)	22.3	0.33	0.26	0.40	1.30	?
(2)	24.9	0.33	0.27	0.44	1.20	36
(3)	26.9	0.33	0.25	0.39	1.35	44
(4)	34.	—	—	—	1.33	?
(5)	52.	0.25	0.21	0.56	1.24	47

[1] K = knots or nodes per whorl.

(1–4) *C. barwicki*, n.sp., pl. 58, fig. 10(1), figs. 13, 14(2), figs. 11, 12(3), fig. 15(4).

(5) *Anolcites armatum* (Münster) Mojsisovics, 1882, p. 100, pl. 34, figs. 2, a,b.

Evolute, discoidal, ribbed forms with the suggestion of a ventral furrow caused by small knots on the ends of the ribs. Whorls are higher than wide, with an abrupt umbilical shoulder. Ventral shoulder gradational, not abrupt. Cross section of whorls helmet-shaped. Outer whorl embraces perhaps one-third of inner.

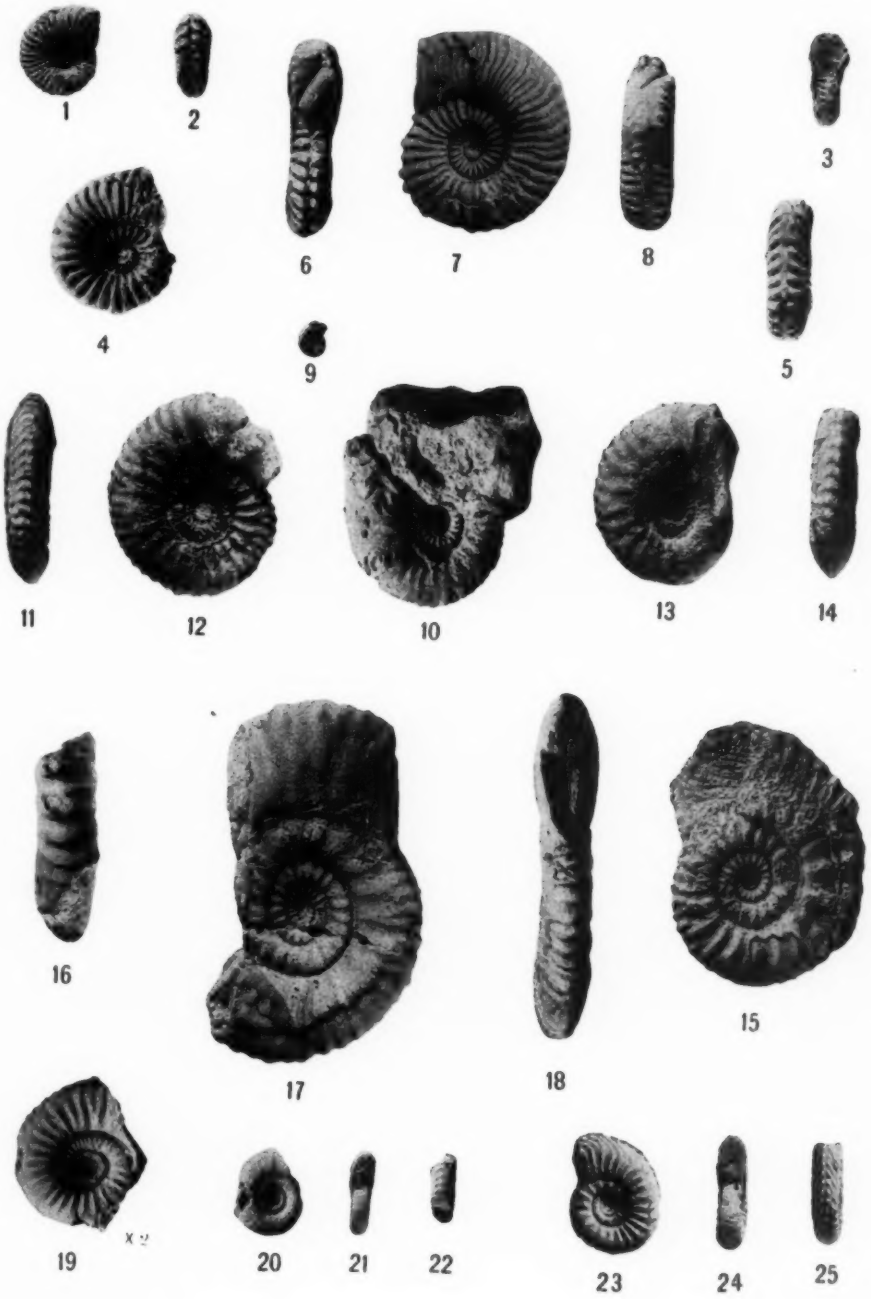
Ribs run almost straight from the umbilicus to the venter. Each rib either forks or has another rib, not extending umbilically from the middle of the flanks, intercalated between itself and the next main rib. In this manner, there are always two ribs on the venter for one at the umbilicus. As each rib has a small knot bordering the ventral depression, the number of these knots also is double that of ribs at the umbilicus. None

EXPLANATION OF PLATE 58

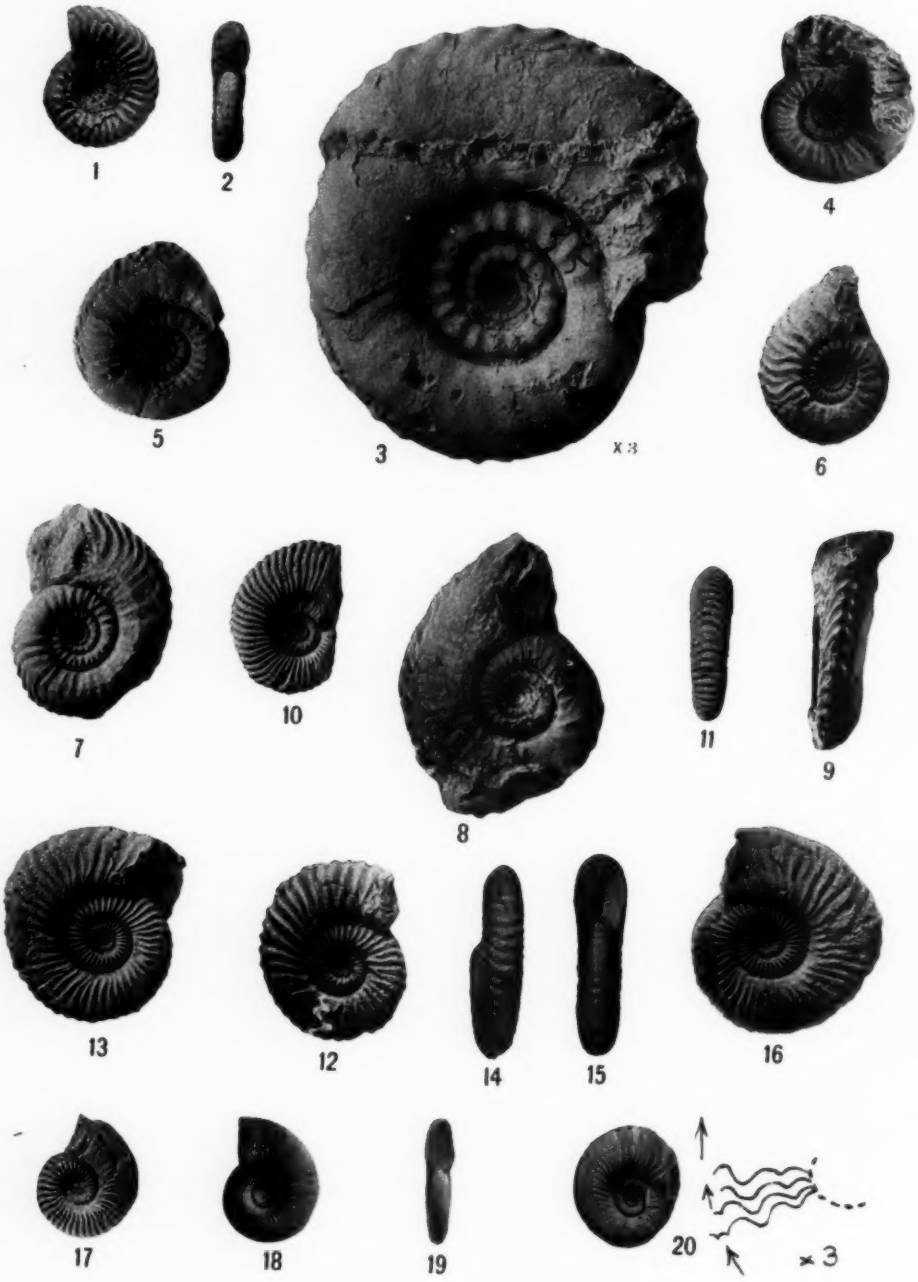
FIGS. *1–8—Clionites wheeleri* Johnston, n. sp., *1–3*, D = 13.0 mm. *4–5*, D ≙ 20.2 mm., *6–8* Holotype, D = 28.0 mm. U. S. Nat. Mus. 77511. (p. 449)

9–18—Clionites barwicki Johnston, n. sp. *9*, D = 5 mm., represents the inner whorls of *10*, D = 22.3 mm., and is drawn, ×2, in text fig. 1A. *13–14*, D = 24.9 mm. *11–12*, D = 26.9 mm. *15*, D = 34 mm. *16–18*, D = 48.4 mm. U. S. Nat. Mus. 77512. (p. 450)

19–25—Clionites reesidei Johnston, n. sp. *19*, D = 10 mm.; ×2. *20–22*, D = 11.6 mm. *23–25*, D = 16.0 mm. U. S. Nat. Mus. 77513. (p. 451)



Johnston, Triassic Cephalopods



Johnston, Triassic Cephalopods

of the ribs show the abrupt forward bend on the ventral shoulders of the related species *Clionites reesidei*, n. sp.

The "ventral furrow" is not a true furrow, as it does not sink in below the interrib spaces. In fact, it does not even sink below the ribs, which continue uninterrupted over the venter as on *Anolcites*, a subgenus of *Trachyceras*. The impression of a ventral furrow is entirely due to small knots forming two spirals on either side of the middle of the venter.

This species resembles the mature form of "*Trachyceras*" *armatum* (Münster) Mojsisovics (1882, p. 101, pl. 34, figs. 2a, b) but not the young forms with spines on the flanks (pl. 23, figs. 35, 36). Later included by Mojsisovics in his subgenus *Anolcites* (1893, p. 622) and so regarded by Diener and Kutassy in the "*Fossilium Catalogus*" (1915, p. 287; 1933, index, p. 763), Kittl nevertheless pointed out the strong resemblance to *Clionites* on account of its evolute form (1908, p. 490). It also has only one spiral of knots or spines, and the whorls increase slowly in height. The ribs on mature forms seem similar in trend to those of *C. reesidei* but do not fork so much. Proportions differ as shown in the above table. The sutures seem similar in numbers and arrangement of elements. Mojsisovics describes them as follows:

> The second lateral saddle is on the edge of the umbilicus. Saddles entire, rounded. External (ventral) lobe shorter than the first lateral, divided by the "Median-höcker" (median saddle) into two blunt, unserrated points. First lateral lobe narrow, with three small serrations on the end, second lateral lobe running together into a single point.

The sutures of the mature form from Nevada correspond exactly with Mojsisovic's description and illustration (pl. 34, fig. 2a) except that the second lateral lobe is rounded, not pointed.

It was possible to break out the inner whorls from the specimen of 22.3 mm. D. To a diameter of about 10 mm. the whorls are about as wide as high (text figure 1A). Then the height increases faster than the width. At 5 mm. D the lobes are unserrated, goniatitic. Ventral lobe divided; first lateral lobe pronounced and is the largest lobe; second lateral barely suggested. Ribs pronounced on umbilical shoulder, becoming very faint in middle of the flanks, and leaving just a suggestion of the ventral knots of mature forms at their ends. Within one volution *apicad* (toward the apex or protoconch, in distinction to *orad*, towards the aperture or living chamber) the ribs die out on the flanks and there are no more ventral knots. The second lateral lobe has not yet appeared. A tiny section, which would fit orad on the above, shows the internal sutures. A lobe, smaller than the second lateral, is crossed by the suture of involution (line of contact of outer whorl with inner whorl). A small saddle follows, then a dorsal lobe. There is little or no resemblance between the young "*Trachyceras*" *armatum* (Mojsisovics, 1882, pl. 24, figs. 35, 36) and *Clionites barwicki* of less than 10 mm. diameter.

Length of living chamber at least one-half whorl.

This species is named in honor of Professor Arthur R. Barwick of the Catholic University of America.

CLIONITES REESIDEI
Johnston, n. sp.
Plate 58, figures 19–25; plate 59, figures 1–9; text figures 1B, C

	D	H/D	W/D	U/D	H/W	
(1)	10.0	0.35	0.31	0.39	1.13	25 R^1
(2)	11.6	0.34	0.28	0.41	1.18	—
(3)	16.0	0.34	0.24	0.44	1.45	—
(4)	19.1	0.35	0.26	0.42	1.34	—
(5)	20.	—	—	—	—	—
(6)	21.2	0.35	0.23	0.44	1.54	—
(7)	21.6	0.37	0.24	0.40	1.33	43 K^2
(8)	24.1	0.35	0.22	0.40	1.56	37 K

EXPLANATION OF PLATE 59

FIGS. *1–9—Clionites reesidei* Johnston, n. sp. *1–2*, holotype, D=19.1 mm. *3*, D=ca. 20 mm., ×3. *4*, D=21.2 mm. *5*, D=21.6 mm. *6*, D=24.1 mm. *7*, D=27.6 mm. *8–9*, D=30.0 mm. U. S. Nat. Mus. 77513. (p. 451)

10–16—Hannaoceras newpassense Johnston, n. sp. *10–11*, D=21 mm. *12*, D=24 mm. *13–16*, D=26 mm., holotype. U. S. Nat. Mus. 77514. (p. 454)

17–20—Lecanites trauthi Johnston, n. sp. *17*, D=15.0 mm. *18–19*, D=16.4 mm. *20*, D=16.3 mm., holotype, with drawing of sutures, ×3. U. S. Nat. Mus. 77515. (p. 455)

	D	H/D	W/D	U/D	H/W		
(9)		27.6	0.38	—	0.39	—	—
(10)		30.0	0.35	—	0.44	—	—
(11)		16.5	0.39	0.21	0.33	1.63	—

[1] R = ribs per whorl.
[2] K = knots or nodes per revolution.
(1–10) *C. reesidei*, n.sp. pl. 58, fig. 19 (specimen shows sutures) (1); figs. 20–22(2), figs. 23–25(3); pl. 59, figs. 1, 2(4), fig. 3(5), fig. 4(6), fig. 5(7), fig. 6(8), fig. 7(9), figs. 8, 9(10).
(11) *C. valentini* Mojsisovics, 1893, p. 474, pl. 153, figs. 1a-b.

This species differs from *C. barwicki*, n. sp., chiefly in the fact that the ribs take a sharp bend forward (orad) at two-thirds whorl height. On the sutures, the ventral lobe does not have a single point on each half, but two or more points. The second lateral lobe (the last lobe before the umbilical suture) also tends to become serrated. The ribs show less tendency to division and practically none are intercalated.

At 10 mm. D the two halves of the divided ventral lobe are already serrated, and the second lateral lobe is present. The latter is added in one revolution, springing away from the umbilical suture. The ventral knots defining the ventral "furrow" already are present but diminish apicad. The ribs are strongest from the umbilicus to the forward bend, where they become fainter.

The specimen of 11.6 mm. D has the shell preserved at the beginning of the last volution. No ventral knots are present before the end of this volution, although striae of growth show a forward bend like that of the ribs on larger specimens. Ribs are extremely faint, especially on the inner volutions, where they are more widely spaced. The living chamber is at least one-half revolution long.

At 16 mm. D, ventral knots ending the ribs are clearly defined. There are 23 ribs per revolution at the umbilicus. At least 25 ventral knots were counted in three-fourths of a revolution. The increase in number of knots at the venter over ribs at the umbilicus is due to (1) forking of the ribs at one-fourth whorl height, (2) forking of the ribs at two-thirds whorl height, and (3) intercalation of ribs extending from the forward bend onto the venter. The second case is the most frequent. Sometimes an intercalation occurs between a fork.

The specimen of 19.1 mm. D has saddles on the suture line that are somewhat wavy. Ribs are strong. There are fewer forkings and intercalations than on the preceding specimen: most of the ribs are single, unforked. The beginning of the living chamber is seen. This specimen is chosen as the type.

20 mm. D: Three lateral lobes of the suture are clearly seen. The ribs are somewhat weaker than usual.

21.2 mm. D: Some of the ribs bend backwards first, then forward, assuming somewhat the shape of a question mark. There is a suggestion of knots on the ventral shoulders due to strengthening of the ribs at this point, followed by a weakening before the ventral knots.

21.6 mm. D: All lobes are serrated. The ribs on the flanks are weak, except at younger stages. The living chamber is at least one-half revolution long.

24.1 mm. D: The ribs are very fine. The living chamber is at least one-half revolution long.

27.6 mm. D: The shell is preserved almost entirely. The ribs seem coarser than average. The ventral "furrow" is, as usual, outlined

EXPLANATION OF TEXT FIGURE 1

A, *Clionites barwicki* Johnston, n. sp. Inner whorls of pl. 1, fig. 10. The lower figure is a drawing of pl. 58, fig. 9, ×2, showing the sutures. (p. 450)
B, *Clionites reesidei* Johnston, n. sp. Sutures of pl. 59, figs. 1, 2, the type, ×3. Penciled lines indicate trend of ribs. (p. 451)
C, *Clionites reesidei* Johnston, n. sp. Sutures of pl. 59, fig. 5, ×3. (p. 451)
D, *Hannaoceras newpassensis* Johnston, n. sp. Sutures of pl. 59, fig. 5, ×3. (p. 454)
E, *Arpadites* (*Arpadites*) *schencki* Johnston, n. sp. Sutures of pl. 60, fig. 1, 2, the type, ×3. Straight dashed lines indicate the ventral keels. (p. 458)
F, *Perrinoceras novaditus* Johnston, n. sp., n. gen. Sutures of pl. 60, figs. 3, 4, the type, ×1. (p. 460)
G, *Metahedenstroemia? desertorum* Johnston, n. sp. Sutures of a fragment of 19 mm. whorl height. Dotted lines near the arrows indicate the two ventral keels or flanges. Note lack of symmetry of the suture on the two sides of the median arrows.
H, *Metahedenstroemia? desertorum* Johnston, n. sp. Drawing of pl. 61, fig. 4, ×1. (p. 460)

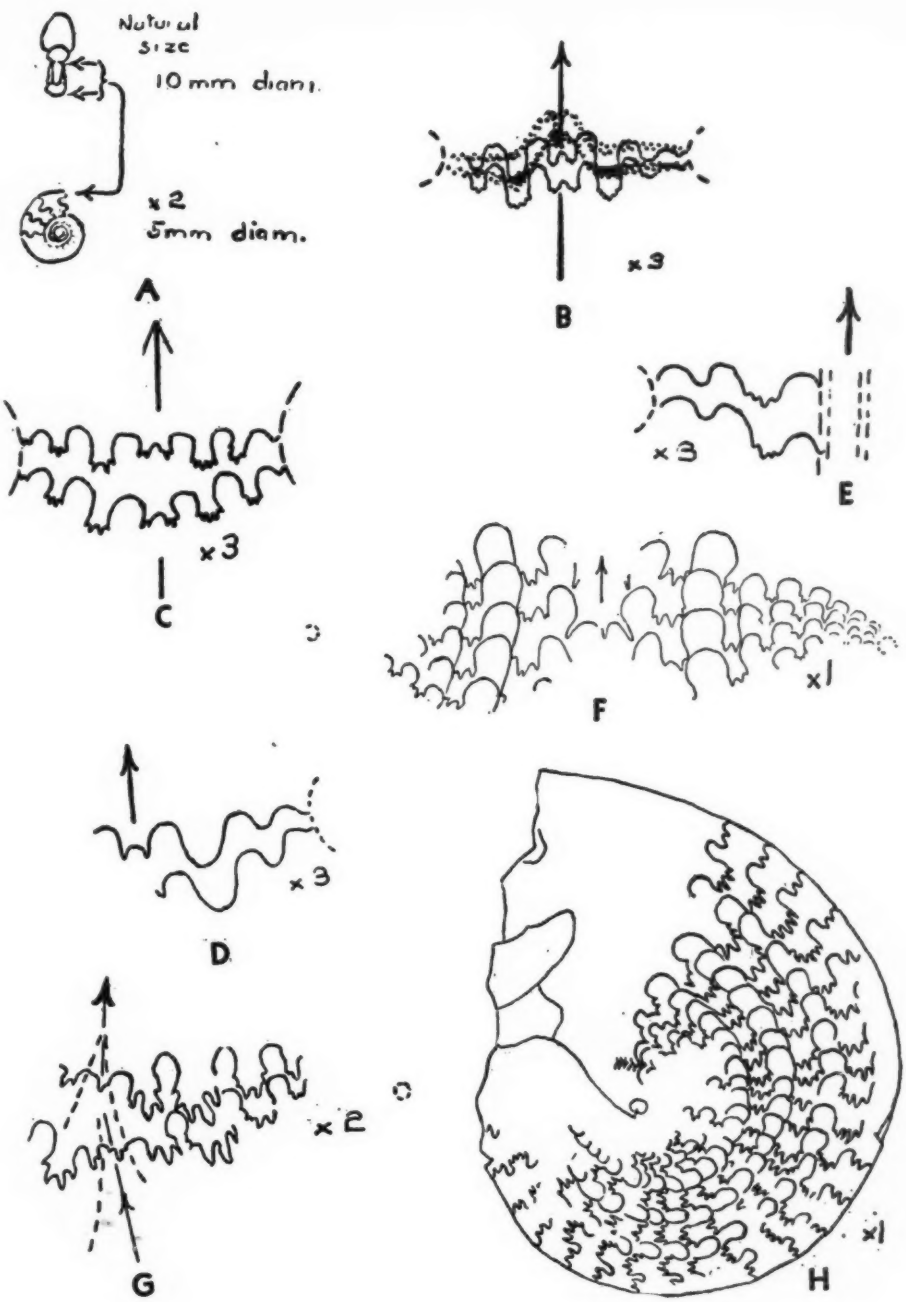


FIG. 1—Sutures of ammonites.

by the ventral knots, but ribs cross the furrow, nevertheless, between opposite knots, suggesting *Trachyceras* (*Anolcites*).

30.0 mm. D: This is the largest specimen collected. It is complete except for the aperture: the living chamber is at least three-quarters of a revolution long. The ribs are fine, especially towards the end of the living chamber. Here there is also the suggestion of knots on the ventral shoulder.

These Nevada specimens strongly resemble forms like *Clionites angulosus* and its relatives, especially *C. valentini* Mojsisovics (from the zone of *Lobites ellipticus* of the Hallstatt limestone of the Feuerkogel on the Röthelstein near Aussee, Austria) from which it differs only in details of sculpture and in slightly greater compression. The sutures of *C. valentini* are not known, but the sutures of *C. angulosus* are described as:

> Ventral lobes lower than the first lateral, with a small median saddle and weak indications of teething on both halves. First lateral lobe three-pointed; second flatly rounded, with weak traces of teething, lying on the umbilical shoulder. (Translation.)

This species is named in honor of Dr. John Bernard Reeside, Jr., of the United States Geological Survey, who has assisted the author a great deal in this work.

Genus HANNAOCERAS Tomlin

Polycyclus MOJSISOVICS, *1893*, p. 534; HYATT and SMITH, *1905*, p. 201; DIENER, *1915*, p. 226; SMITH, *1927*, p. 96; KUTASSY, *1933*, p. 620.
Smithoceras HANNA, *1924*, p. 180.
Hannaoceras TOMLIN, *1931*, p. 174.
Polysphinctoceras SPATH, *1934*, p. 198 footnote.

Genotype: *Ammonites nasturtium* Dittmar, 1866.

Geographic range: Alpine-Mediterranean and Himalayan regions; California, and New Pass, Nevada.

Geologic range: Karnic (and Noric?).

Characteristic features of this genus are its general shape (widely umbilicate, laterally compressed, with whorls growing very slowly in height) combined with rather straight radial ribs running from umbilical suture to umbilical suture without interruption at any point, whether on the venter or elsewhere, combined with a very simple suture line. This suture line consists of a ventral lobe divided into two prongs by a small siphonal saddle; a large first lateral lobe, which may be either unserrated or slightly serrated; a second smaller lobe, which is not serrated; and perhaps a suggestion of a very small third lobe near the umbilical suture.

The specimens from New Pass have no serrations on the lobes. *Hannaoceras major* (Smith) (1927, p. 97, pl. 58, fig. 32) not only has incipient serration of the large lateral lobe but also serration on the outside of the two prongs of the ventral lobe. The sole suture of the type species illustrated by Mojsisovics (1893, pl. 132, fig. 34c) shows no incipient serration of the main lateral lobe. The latter is rounded. This statement is confirmed by the description on p. 536. On the other hand, *H. henseli* Oppel is said to be weakly toothed (p. 537).

There seems to be some confusion regarding the proper name of the genus. Lamark in 1815 gave the name *Polycyclus* to a genus of tunicates (ascidians), hence the name was preoccupied when Mojsisovics used it in 1893 for his ammonites. Hanna, 1924, proposed a new name, *Smithoceras*, for Mojsisovics' genus but this also was preoccupied. Tomlin, realizing this fact, proposed *Hannaoceras* in 1931. Later Spath, 1934, for what reason I do not know, proposed *Polysphinctoceras* for the same genus. Unless *Hannaoceras* itself is preoccupied, it is the valid name.

HANNAOCERAS NEWPASSENSE Johnston, n. sp.

Plate 59, figures 10–16; text figure 1D

	D	H/D	W/D	U/D	H/W	R[1]
(1)	21	0.33	0.29	0.41	1.17	—
(2)	24	0.33	0.25	0.45	1.33	—
(3)	26	0.33	0.27	0.46	1.21	44
(4)	30	0.30	0.20	0.47	1.50	50
(5)	28	0.27	0.25	0.50	1.07	—
(6)	11	0.34	0.24	0.35	1.42	—
(7)	14	0.32	0.24	0.43	1.37	—

(1–4) *H. newpassense*, n.sp., pl. 59, figs. 10, 11(1), fig. 12(2), figs. 13–15(3).
(5) *H. ernesti* Mojsisovics, 1893, p. 540, pl. 132, fig. 25.
(6) *H. lucii* Mojsisovics, idem., fig. 24.
(7) *H. rothpletzi* Mojsisovics, idem., fig. 26.
[1] R = ribs per whorl.

Number of specimens studied, 29.

The general form is discoidal, evolute, with whorls little-embracing and increasing

slowly in height: the height is multiplied about 1.7 times per revolution. The umbilicus is open, shallow, and with abrupt shoulders and vertical sides. The whorls are higher than wide: H/W varies from 1.2 to 1.5. The ornamentation consists of the characteristic radial ribs running over the venter without interruption. These ribs are generally simple, unforked, although they may fork on the umbilical shoulder or near the venter. The ribs are fine, numerous, and no wider than the interspaces.

The sutures are goniatitic. The ventral lobe is divided into two points by a small siphonal saddle. The first lateral lobe is the largest. It is rounded, unserrated. The second lateral is smaller. There may be a still smaller lobe cut by the umbilical suture.

J. P. Smith (1927, pp. 96–97) gives three species of *Hannaoceras* from the zone of *Tropites subbullatus* in Shasta County, California, namely, "*Polycyclus*" *nodifer* Hyatt and Smith, "*P.*" *henseli* Oppel, and "*P.*" *major* Smith. All of these show a tendency towards serration of the first lateral lobe, which the Nevada species never shows. Besides, there are never any nodes on the venters of the Nevada forms.

Mojsisovics (1893) described three species from the *Lobites ellipticus* zone of the Feuerkogel near Aussee, Austria, all of which resemble the Nevada species in a general way. The sutures of none of these are known in detail. None show any forking of the ribs, nor do the latter bend forward on the venter as much as on some of the Nevada forms. *H. ernesti* Mojsisovics is sufficiently distinguished from the rest by the flattened venter. The proportions of these three species are given in the above table.

The more diagnostic features of the new species might be summarized as follows: (1) All the lobes, even the first lateral, are unserrated. (2) The ribs generally bend slightly forward on the venter. (3) The ribs generally run without forking from umbilical shoulder to umbilical shoulder but may fork on this shoulder or on the flanks. On the specimen of 24 mm. D one rib forks above the middle of the flanks. The specimen of 21 mm. D shows no forked ribs.

The specimen of 26 mm. D is chosen as the type.

Genus LECANITES Mojsisovics

Lecanites MOJSISOVICS, *1882*, p. 199; HYATT and SMITH, *1905*, p. 137; SMITH, *1914*, p. 65.

Type: "*Ammonites*" *glaucus* Muenster 1834 p. 11, pl. 1, fig. 1.

Geographic range: Alpine-Mediterranean region and Nevada.

Geologic range: Anisic-Karnic.

Smith's discussion of this genus is adequate. The type species of the genus is figured by Mojsisovics (1882), pl. 30, figs. 1–6). For other references, see Diener's catalogue.

LECANITES TRAUTHI

Johnston, n. sp.

Plate 59, figures 17–20

	D	H/D	W/D	U/D	H/W
(1)	15.0	0.33	—	0.37	—
(2)	16.3	0.37	0.26	0.37	1.43
(3)	16.4	0.42	0.26	0.27	1.62
(4)	12	0.33	0.17	0.42	2.00
(5)	32.3	0.38	0.20	0.33	1.15
(6)	30.7	0.26	0.19	0.53	1.40
(7)	23.5	0.34	0.25	0.43	1.38
(8)	30.5	0.36	0.20	0.39	2.00
(9)	43.1	0.27	0.23	0.50	1.15
(10)	34.3	0.31	0.25	0.47	1.24
(11)	23.0	0.32	0.27	0.44	1.20
(12)	21.7	0.36	0.25	0.42	1.42
(13)	36.6	0.21	—	0.55	—
(14)	37.6	0.30	—	0.36	—
(15)	46.	0.39	0.23	0.33	1.71

(1–3) *L. trauthi*, n.sp., pl. 59, fig. 17(1) (shows ribs), figs. 18, 19(2) (type, shows sutures), fig. 20(3) (shows sutures).
(4) *L. glaucus* (Münster) Mojsisovics, 1882, p. 200.
(5) *L. crassus* Smith, 1914, p. 66, pl. 89, figs. 1, 2.
(6) *L. parvus* Smith, 1914, p. 66, pl. 30, figs. 25, 26.
(7) *L. nudus* Smith, 1914, p. 66, pl. 98, figs. 8, 9. Measurements from the plate.
(8) *L. vogdesi* Hyatt and Smith, 1905, p. 139, pl. 60, figs. 12–14.
(9–12) Same species in Smith, 1914, p. 67, pl. 30, fig. 17(9), figs. 18, 19(10), fig. 20(11), and pl. 75, fig. 10(12).
(13) *L. sybillinus* Frech, 1911, p. 17, pl. 2, fig. 4. Measurements from plate.
(14) *L. loczyi* Frech, 1911, p. 45, pl. 10, fig. 4, text fig. 14. Measurement from plate.
(15) *L. spitzbergensis* Frebold, 1929, p. 299, pl. 1, fig. 1.

Number of specimens studied, nine.

Evolute, discoidal, laterally compressed forms increasing rapidly in height (100 per cent per revolution). All of the last revolution (D = 15 mm.) and at least half of the preced-

ing are finely ribbed. The ribs are flame-shaped, broadening towards the venter which they do not seem to cross. They arch slightly backwards on the flanks, forwards more sharply on the ventral shoulders. The venter is somewhat sharpened though not acute. Outer whorl embraces one-fourth of inner whorl. Aperture follows trend of ribs, except that it projects slightly forwards near umbilical suture. Ventral lappet is present. Living chamber is three-fourths revolution long.

Sutures are goniatitic, with three rounded saddles and two rounded lobes. Ventral lobe is divided by a small median saddle into two pointed halves.

The Nevada specimens are wider in proportion to diameter than *L. glaucus* Münster, the genotype (see Mojsisovics, 1882, p. 200), and the ribs are stronger judging from Mojsisovic's description. Sutures agree fairly well with Laube's figure 9 (1869b, pl. 37).

Lecanites crassus Smith (1914, p. 66, pl. 89, figs. 1, 2) is much more robust than *L. trauthi*, its involution is slightly greater, and the ornamentation is very different (pronounced, widely spaced ribs at the umbilicus which die out on the flanks, not crossing the venter). The ventral lobe is divided, but the two halves are rounded, not pointed. Whorls increase in height about 100 per cent per revolution, like *L. trauthi*.

Lecanites parvus Smith (1914, p. 66, pl. 30, figs. 25–27) does not grow as rapidly in height of whorl and lacks the radial ribs of *L. trauthi*. The septa of the former (pl. 30, fig. 27) are from a specimen almost 8 mm. in diameter which, compared with an *L. trauthi* of equal diameter, shows a more gently rounded, less acute venter and no ornamentation resembling the strong falcoidal ribs of the latter. Smith's type shows part of similar septae, also radial growth lines. The divided ventral lobe has rounded ends.

Lecanites nudus Smith (1914, p. 66, pl. 98, figs. 8–12) has a nearly smooth surface with weak umbilical folds that extend up the flanks as striae of growth, and not like the strong radial ribs of *L. trauthi*. It is more robust.

Lecanites vogdesi Hyatt and Smith (see Smith, 1914, p. 67, pl. 10, figs. 12–22; pl. 12, figs. 10–13; pl. 30, figs. 17–24; pl. 88, figs. 24, 25), at comparable diameters, has wider and lower whorls than *L. trauthi*. The ribs are more widely separated, coarser, and do not extend as far over the sides as on the new species. Plate 88, figs. 24, 25, has the finest sculpture of all but still suggests the coarse, umbilical, widely spaced type.

Lecanites sybillinus Frech (1903, p. 17, pl. 2, fig. 4) has whorls lower in proportion to diameter than *L. trauthi*, a wider umbilicus, whorls less embracing and increasing less rapidly in height. It shows no surface sculpture: the shell is smooth.

Lecanites? spitzbergensis Frebold (1929, p. 299, pl. 1, fig. 1), according to the illustration, has more embracing whorls than *L. trauthi:* the last whorl embraces two-thirds of the preceding. The ribs seem broader, more widely spaced, and less numerous.

Lecanites loczyi Frech (1903, p. 45; pl. 10, fig. 4; text fig. 14) has the vestige of a third lateral lobe on the flanks, unlike any other European *Lecanites* or the new species. It has distinct falcoidal radial ribs like the new species but is more involute.

To sum up, the new species seems to have a narrower umbilicus in relation to diameter than any hitherto described species except *L. crassus* Smith, a more robust form, *L. loczyi*, and *L. spitzbergensis;* and more pronounced, numerous, and finer falcoidal radial ribs than any of its brethren.

It is named in honor of Herr Doktor F. Trauth of the Naturhistorischen Museum in Vienna.

Genus ARPADITES Mojsisovics

Arpadites MOJSISOVICS *1879*, p. 140 (part); *1882*, p. 52 (part); *1893*, p. 450 (part).—TORNQUIST, *1898*, p. 647.—HYATT and SMITH, *1905*, p. 174.—SMITH, *1927*, p. 93.—YABE and SHIMIZU, *1927*, p. 17 (or 117).

Type: *Ammonites arpadis* Mojsisovics, 1870.

Geographic range: Alpine-Mediterranean, Himalayan, and East-Pacific regions.

Geologic range: Ladinic, Karnic, and Noric.

Subgenera: *Arpadites* s.s., *Asklepioceras*, *Dittmarites*, and *Trachypleuraspidites*.

Mojsisovics first described the genus in 1879 as follows:

. . . distinguished by a deep furrow in the middle of the venter and by a long single-pointed anti-

siphonal lobe. Often smooth or knotty keels border the ventral furrow, but on some forms the ribs end at the furrow simply with a thickening. Numerous simple or dichotomizing ribs, which always begin at knots on the umbilicus (umbilical shoulders?) adorn the sides, on which additional rows of knots may arise. The geologically older forms have high, rounded saddles and finely toothed lobes; on a number of younger St. Cassian forms, also the saddles are serrated.

Mojsisovics mentions in this description the following species of *Arpadites:*

arpadis Mojsisovics (*Arpadites* s.s.)
szaboi Böckh (*Arpadites* s.s.)
manzonii Benecke (*Arpadites* s.s.)
achelus Münster (not *Arpadites* but *Klipsteinia*)
brevicostatus Klipstein (same as *A. sulcifer* Münster.)
sulciferum Münster (not *Arpadites* but *Trachyceras*)
rüppeli Klipstein (*Dittmarites*)
sesostris Laube (*Dittmarites*)
hirschi Laube (not *Arpadites* but *Klipsteinia*)
hörnesi Hauer (type of genus *Steinmannites* Mojsisovics, 1893)
laubei Mojsisovics (same as "*Arpadites*" *rüppeli* Hauer)
rüppeli Hauer (not *Arpadites* but *Clionites*)

Both from the description and from the list of species it is clear that Mojsisovics did not originally exclude from the genus forms *without* two distinct keels bordering the ventral furrow, such as are now placed in the genera *Klipsteinia* (*K. Natalia* Mojsisovics, however, has two crenulate keels bordering the ventral forrow), *Trachyceras* (*Trachyceras* s.s.), *Steinmannites*, and *Clionites*.

In 1882 Mojsisovics limits the genus to forms with a median furrow bordered by ventral keels, which, however, may not yet be present on the inner whorls. He recognized two lateral lobes on such forms. Sutures are ceratitic (older beds) or ammonitic (younger beds of the zone of *Trachyceras aon*). The second lateral lobe may be one-or-more-pointed or end in a pointed arch. The dorsal lobe was observed on one specimen to be one-pointed, but might be several-pointed on other specimens. With the exception of the species *liepoldti* Mojsisovics, recognized by Diener as a true ceratite on account of having three lateral lobes instead of two as on *Arpadites* and on account of lacking true keels, the species included by Mojsisovics in *Arpadites* in this work are still so included.

In 1893 Mojsisovics still included under *Arpadites* as subgenera groups which Diener and later workers have considered as independent genera, such as *Münsterites* (Karnic), *Clionites* (Ladinic?, Karnic, Noric), *Steinmannites* (Noric), *Daphnites* (Noric and neo-Trias of Sicily), *Dionites* (Noric) (Mojsisovics calls this a genus: p. 453) and *Drepanites* (Noric) (a genus: Mojsisovics, p. 453.) "*Arpadites*" *segmentatus* Mojsisovics, which Renz later made the type of the subgenus Asklepioceras, has no ventral keels although it does have the ventral furrow.

Tornquist, 1898, lists under *Arpadites* the following: *A. cinensis* Mojsisovics, *A. telleri* Mojsisovics, *A. arpadis* Mojsisovics, *A. venti-settembris* Tornquist, and *A. trettensis* Mojsisovics.

Hyatt and Smith, 1905, define the genus as having a ventral furrow bounded by shoulder keels. The so-called "*Arpadites*" *gabbi* of Hyatt and Smith, however, has no keels of any kind bordering the ventral furrow. The ontogeny of the species is shown on their plates 38 and 39. The youngest forms are broad-ventered, widely umbilicate, without furrows or keels on the venters. Towards maturity they acquire a median ventral furrow but no keels. The venter becomes narrower and narrower in proportion to the height of the whorl. The suture of the most mature specimen differs from that of *Arpadites* s.s. in having two serrated auxiliary lobes (pl. 39, fig. 3) instead of one or none, but these occur at about 56.9 mm. diameter, a diameter notably greater than that of any other described member of this genus. In fact, only *A. telleri* (D = 49 mm.) and *A. cinensis* var. *alta* (D = 48 mm.) approach it in size. At lesser diameters (D = 41 mm.; pl. 39, figs. 4–7) the suture is more the usual one for *Arpadites*.

Smith's 1927 work repeats the above generic definition, also the description and illustrations of *A. gabbi*. He adds one new species, "*Arpadites*" *kingi*, very similar to *A. gabbi* and like it without ventral keels. The suture cannot be seen on the originals of the illustrations of *A. kingi*.

I suggest that Smith's species, which do

not resemble *Arpadites* s.s. on account of the lack of ventral keels at all stages of growth, be placed in a new genus, for which the name *Trachystenoceras* is proposed. *Asklepioceras*, a subgenus of *Arpadites*, which also has no ventral keels, has a simpler suture line. There is considerable resemblance to some members of *Paratrachyceras*, subgenus of *Trachyceras*, and especially to *Paratrachyceras laricum* Mojsisovics (1882, pl. 24, figs. 4a, b).

If there is anything in palingenesis, of which Dr. Smith was an advocate, and if "*Arpadites*" *gabbi* did descend from the true *Arpadites* of older horizons, its young forms should show characters of these true *Arpadites*. One of the most diagnostic of these characters is the presence of two keels bordering the ventral furrow. Such keels are never present on "*Arpadites*" *gabbi* at any stage of its development. This is a reason for making a new genus of this form and its relative, "*Arpadites*" *kingi*, instead of making it a subgenus of *Arpadites*.

Hisakatsu Yabe and Saburo Shimizu add nothing new to the definition of the genus, but make some remarks on its distribution in Japan.

In Diener's catalogue (1915, p. 53) the genus is divided into the subgenera given above. Of these *Asklepioceras* Renz (1911, p. 71) (one Ladinic species, four Karnic) has no ventral keels. *A. helenae* Renz (1911, pl. 4, fig. 4c) shows the simplified suture line mentioned in the original subgeneric description (1911, p. 71): saddles are rounded, principal lateral lobe has three points, ventral lobe has two, second lateral has one. *Arpadites segmentatus* Mojsisovics, however, indicated as the type species of the subgenus, is described by Mojsisovics (1893, p. 457) as having saddles with sacks (ammonitic suture?).

The remaining subgenera all have a pair of keels separated by the ventral furrow. *Arpadites* s.s. (Ladinic, Karnic) has ceratitic sutures (saddles entire, rounded) except *Arpadites rimkinensis* Mojsisovics (1896, p. 622, pl. 14, figs. 6a, b) which probably should be included in *A.* (*Dittmarites*) on account of the "brachyphyllic" saddles which Mojsisovics compares to those of *Arpadites* (*Dittmarites*) *ladon* Mojsisovics (1893, pl. 153, figs. 6, 7). *Dittmarites* Mojsisovics (1893 p. 451, Ladinic?, Karnic, and Noric) and *Trachypleuraspidites* Diener (1906, p. 48, Karnic-Noric) have ammonitic sutures on mature forms, with serrated saddles, although *A. rimosus* Münster (Mojsisovics, 1882, pl. 25, fig. 12)—a small individual but type of *Dittmarites*—apparently has ceratitic sutures. This subgenus differs from *Trachypleuraspidites* chiefly in the absence of knots and spines, which are strongly developed on the latter.

KEY TO SUBGENERA OF ARPADITES

1. No ventral keels.....*Asklepioceras.*
1. Ventral keels.
   2. Sutures ceratitic.....*Arpadites* s.s.
   2. Sutures ammonitic.
      3. Spines and tubercles on the ribs. .....*Trachypleuraspidites.*
      3. No spines or tubercles on the ribs. .....*Dittmarites.*

ARPADITES SCHENCKI
Johnston, n. sp.
Plate 60, figures 1, 2, text figure 1E

	D	H/D	W/D	U/D	H/W
(1)	26		0.39	0.25 0.17	1.08
(2)	26	0.44	0.31	0.25	1.44

(1) *A. schencki*, n.sp. As the specimen is somewhat distorted, and the two sides are not alike, the proportion U/D has been given for both sides.
(2) *A. stracheyi* Mojsisovics, 1896, p. 621 and the text figure.

The following description applies to the

EXPLANATION OF PLATE 60

FIGS. *1, 2*—*Arpadites* (*Arpadites*) *schencki* Johnston, n. sp. D=26 mm., holotype. U. S. Nat. Mus. 77517. (p. 458)
3–5—*Perrinoceras novaditus* Johnston, n. sp., n. gen. *3–4*, D=ca. 95 mm., holotype. *5*, A septate fragment. U. S. Nat. Mus. 77516. (p. 460)
6–8—*Metahedenstroemia? desertorum* Johnston, n. sp. *6–7*, D=24 mm. *8*, D=37 mm. U. S. Nat. Mus. 77518. (p. 460)
9, 10—*Sageceras* cf. *S. haidingeri* Hauer. H=15 mm. U. S. Nat. Mus. 77519. (p. 462)

Johnston, Triassic Cephalopods

Johnston, Triassic Cephalopods

only specimen so far studied in detail. (Two specimens of not more than 10 mm. D, the smaller one showing sutures, are at Stanford University, Calif.) It is imperfect, somewhat distorted, but shows at least the beginning of the living chamber, some of the shell with its ornamentation, and the sutures.

The general shape is discoidal, rather involute. The whorls seem to increase in height rather rapidly: 1.4 to 1.5 times in one half revolution, not allowing for the distortion. Inner whorls have arched flanks curving into the rounded ventral region; outer whorls are apparently more compressed laterally. The umbilicus is open, shallow, but with abrupt shoulders. The ornamentation consists of very fine radial striations superimposed on broader, very shallow, radial folds, which have the same trend as the striations, running straight up the flanks from the umbilical shoulders to one-third or three-fourths of the whorl height, where they are arched forward (orad) at about 45° to the radius and merge, without interruption by any lateral furrows, into the ventral keels at the most forward part of the whorls giving a slightly crenulate or ribbed appearance to the latter. The median ventral furrow lies between the two keels. It is distinct and visible for the whole of the exposed whorl.

The fine radial striae are visible only on the shell, but the radial folds are also visible on the internal mould. There are no umbilical, lateral or ventral knots, spines, or other protuberances. The living-chamber is at least three-quarters of a revolution long. The sutures have entire rounded saddles, two lobes on the flanks. The first lobe is largest, slightly serrated; the second is smaller, apparently rounded and entire.

This species shows the ventral furrow bordered by two keels and the simple type of suture line characteristic of *Arpadites* s.s. Furthermore, on account of the degree of involution (outer whorl embraces more than half of the inner), it is closer to Mojsisovics' "Gruppe des *Arpadites cinensis*" than it is to the more evolute "Gruppe des *Arpadites arpadis*."

Arpadites schencki, n. sp., is the most involute of all *Arpadites* s.s. so far described. It resembles most closely—so far as can be judged from the description and the illustration of a plaster cast of the original—*Arpadites stracheyi* Mojsisovics (1896, p. 621, text fig.). The type of *A. stracheyi* is said to be in the British Museum and is *Ammonites floridus* juv. Salter (1865, p. 61 pl. 8, fig. 3—others excluded; from Niti Pass, Himalayas; Karnic). It was found with *Hungarites nitiensis* and a *Trachyceras* sp. ind. (group of *duplica*). The form is involute, like the Nevada species, whorls embracing to one-half the whorl height. It also has a relatively weak radial sculpture and ceratitic sutures. Saddles rounded and entire. Lobes serrated, rather shallow; ventral lobe two-pointed, median saddle rudimentary (neither of these exposed on *A. schencki*); a shallow, rounded auxiliary saddle appears outside of the umbilical edge.

This species is named in honor of Professor Hubert Gregory Schenck of Leland Stanford, Junior, University.

Genus PERRINOCERAS Johnston, n. gen.

Genotype: *Perrinoceras novaditus* Johnston, n. sp.

This genus includes ammonites with compressed, involute, discoidal shape and very sharp venter. Sutures are ceratitic. The lobe nearest the venter is pyramidal, either coming to a point or having two small points at its apex.

If the Nevada species (*Metahedenstroemia? desertorum*, n. sp.) which our genotype resembles is really a *Metahedenstroemia*, then our genotype may be a *Parahedenstroemia* Spath (1934, p. 221). The genotype of the latter, *P. acuta* Krafft, which Spath figures (text fig. 70, p. 222), resembles our geno-

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EXPLANATION OF PLATE 61

FIGS. *1–4*—*Metahedenstroemia? desertorum* Johnston, n. sp. *1*, Fragment showing internal sutures, ×4; H = 25 mm. *2*, *3*, Type, D = 50 mm. *4*, D = 72 mm. U. S. Nat. Mus. 77518. (p. 460)

5–9—*Lobites* (*Lobites*) *carinatus* Johnston, n. sp. *5*, D = 17 mm. *g*, D = 21.1 mm. *7–9*, Type, D = 22.5 mm. U. S. Nat. Mus. 77520. (p. 466)

10–14—*Lobites* (*Coroceras*) *zephyrus* Johnston, n. sp. *10*, L = 38.3 mm. *11*, *12*, L = 31.2 mm., type. *13*, *14*, L = 37.4 mm. U. S. Nat. Mus. 77522. (p. 468)

type in general shape, acute venter and in sutures, even to a pyramidal adventitious lobe coming to a point. *Parahedenstroemia*, however, has known representatives only in the lower part of the Lower Trias, whereas our genotype is undoubtedly in the lower part of the Upper Trias. In the same matrix with our type specimen is *Trachyceras*, a genus not known below the Middle Trias. Perhaps *Parahedenstroemia* and *Perrinoceras* are the same, but if this is true, it is strange that no connecting links have been found in the Middle Trias as yet.

PERRINOCERAS NOVADITUS
Johnston, n. sp.
Plate 60, figures 3–5, text figure 1F

On the type specimen (pl. 60, figs. 3, 4, text fig. 1F), the maximum diameter is about 95 mm., H/W is 0.34 at 38 mm. H, and the umbilicus seems to be closed.

Number of specimens studied, three. None of these specimens is complete. The type is still partly embedded in a hard limestone matrix, in which can be seen another fragment of the same species. The third specimen is a fragment showing the acute venter and the adjacent sutures.

The general shape is discoidal, with the venter an acute knife edge, and the umbilicus almost closed. The sides arch gently from umbilicus to venter, without any well-defined umbilical shoulder. In cross section the whorls have somewhat the shape of a spear head. The inner whorl indents about one-third of the outer and is entirely covered by the latter.

The shell is smooth, with fine radial striae of growth. Not enough of the shell is preserved to follow the entire trend of these striae.

The sutures are ceratitic, with rounded saddles and teeth on the ends of the lobes. At a whorl height of 38 mm. eight lobes are observed between the venter and the umbilical suture. The venter cuts a saddle which divides the first lobe into two halves. On the type specimen each half ends in a point, as also is the case with its bed-fellow; but on another fragment each point shows incipient division, one large point showing two small points at its end. The next lobe seems the broadest if not the deepest. It has three to five teeth. The next is a narrower lobe although possibly deeper. It has two to four teeth. The size and number of teeth of succeeding lobes diminish progressively towards the umbilicus. The general trend of the whole suture line is gently convex orad. Suture lines overlap slightly, lobes of a younger suture lying between saddles of an older suture.

The living chamber is at least half a revolution long.

The outstanding features of this species are the knifelike venter and the peculiar single-pointed adventitous or ventral lobe. It somewhat resembles *Metahedenstroemia desertorum*, n. sp., in general shape and in the ceratitic sutures, but the latter has a grooved or flattened venter and an adventitious lobe that is smaller and with more distinct teeth.

Novaditus, the specific name, is a Latinization of New Pass: *novus*—new, *aditus*—a narrow passage.

Genus METAHEDENSTROEMIA Spath

Metahedenstroemia SPATH, *1934*, p. 223.

Genotype: *Hedenstroemia kastriotae* Arthaber (1911, p. 208, pl. 17, figs. 14a–c).

Geographic distribution: Albania, Nevada (South Canyon, New Pass).

Geologic range: Lower Trias (Columbitan?), and Karnic?

See Spath for a description of this genus.

METAHEDENSTROEMIA? DESERTORUM
Johnston, n. sp.
Plate 60, figures 6–8; plate 61, figures 1–4; plate 63, figure 3; text figures 1g, 1h, 2a

	D	H/D	W/D	U/D	H/W	H′/H
(1)	24	0.58	0.25	0.04	2.33	0.79
(2)	37	0.62	—	—	—	—
(3)	47	0.60	0.23	0.03	2.54	0.71
(4)	50	0.60	0.24	0.04	2.50	0.69
(5)	72	0.60	0.19	0.03	3.08	—
(6)	88	0.63	0.24	0.03	2.60	—
(7)	39	0.56	0.13	—	—	—
(8)	46	0.70	0.13	—	—	—
(9)	53	0.53	0.25	0.02	2.16	—
(10)	52	0.56	0.25	0.02	2.32	—

(1–6) *M. desertorum*, n. sp., pl. 60, figs. 6, 7(1), fig. 8(2); pl. 61, figs. 2, 3(4, type), fig. 4(5); pl. 63, fig. 3(6).
(7, 8) *M. kastriotae* Arthaber, 1911, p. 208, pl. 17, figs. 14a–c.
(9, 10) *Arthaberites alexandrae* Diener, 1900, p. 18(9); in Arthaber, 1911, p. 217(10).

Number of specimens studied, 11 fairly complete, 15 fragments.

The general shape of this new species (and genus?) is compressed discoidal, very involute with the umbilicus almost closed. The venter is narrow, not sharpened but flattened or grooved, with angular shoulders. The umbilicus is steep-sided with rounded shoulders. The cross section of the whorls suggests a laterally compressed heart or the head of a spear or arrow. The tabulate venter is already present at about 10 mm. D, but the umbilicus is proportionally much larger here, and the number of sutural elements reduced.

The flanks are very gently arched, almost flat. The shell shows no ornamentation other than falciform radial striae of growth. These striae seem to bundle at regular intervals into faint radial welts.

Growth is very rapid, as the outer whorls are at least three times the height of the inner. In the above table is given the proportion of the height of the outer whorl measured from the venter of the preceding whorl (H′) to the height of the same outer whorl measured from the umbilical suture (H). The proportion varies between 69 and 79 per cent.

The length of the living chamber has not been determined, nor the nature of the aperture. The specimen of D 88 mm. reveals about one-half revolution of the living chamber.

The septae are ceratitic, multilobate, with rounded saddles and toothed lobes. The suture lines overlap, with occasional interference by one suture line with its neighbor. The largest lobe on the specimen of 72 mm. D is the third from the venter. The second from the venter is as well-developed but with shorter sides. The first from the venter—an adventitious lobe—is very variable. At this diameter it consists merely of two short teeth. On one fragment of this species, at H 19 mm., these two teeth are not on the flanks below the ventral shoulder but lie on the venter between the two shoulders. The other side of the ammonite shows the two adventitious teeth in the normal position on the flanks, in other words, the suture line is asymmetrical. The two elements are separated by a saddle on this fragment. On a specimen of D 37 mm. the suture is not lop-sided but one of the two teeth of each pair falls on the venter, the ventral shoulder subdividing each pair. The specimen of D 72 mm, has a saddle traversed by the ventral shoulder, then two more teeth on the venter. This specimen has six other lobes between the principal lateral lobe and the umbilical suture, growing smaller as this suture is approached. The last one is merely a small wedge. In all, on the flanks of this specimen are nine lobes. At 37 mm. D, eight lobes are present.

As Spath, Diener, and others have already pointed out, the number of elements in the suture line increases by addition of adventitious elements (added at the venter) and auxiliary elements (added next to the umbilical suture). The lobes in between grow bigger and more serrated, but there are no intercalations of lobes on the flanks.

The internal suture is clearly visible on one fragment of H 25 mm., H′ 16 mm., which suggests that the next inner whorl had a height of $25-16=9$ mm. With about 10 lobes in the external suture, the internal suture shows six lobes plus one on the dorsum plus one cut by umbilical suture: total eight at most. The lobe next to the dorsum is the largest. The nature of the internal sutures is similar to that of the external. They also overlap.

The name of this species, *desertorum*, refers to the semiarid nature of the country in which it is found.

The author pointed out in his Master's thesis (Stanford, 1930) the resemblance of this species to *H. kastriotae* Arthaber (1911, p. 208, pl. 17, figs. 14a–c). Spath has since made this species the genotype of his genus *Metahedenstroemia* (1934, p. 223). Arthaber's specimens are all thinner in relation to diameter and do not show such a grooved venter as our species. Sutures are similar; both overlap. The Albanian type has seven elements at 39 mm. D, the Nevada species eight or nine elements at 37 mm. D. Can the Nevada specimens, which are undoubtedly of about the same age as the *Lobites ellipticus* fauna of Hallstatt and of the St. Cassian beds (judging from the presence of *Lobites*, *Joannites*, *Trachyceras* cf. *T. aon*, etc.), hence at the base of the Upper Trias,—can these specimens belong

to the same genus as forms from the Lower Trias of Albania? *Procladiscites*, a Middle Triassic form in Europe, has already stretched our credulity.

Professor von Arthaber personally suggested the resemblance of this new species to *Arthaberites alexandrae* Diener known from the *trinodosus* zone (Anisic, Middle Trias) of the Schiechlinghöhe, Austria. Although the general form agrees fairly well in the two species, the sutures of *Arthaberites* do not overlap like those of the Nevada form, and the lobes do not have the parallel sides but show egg-shaped saddles. I also noted that the ventral shoulders of Arthaber's text figure 9 passed between the first prong of the divided ventral or adventitious lobe and the three other prongs of this lobe.

Diener (1900, pl. 2, fig. 4c) shows the same sort of thing. My notes made in Vienna in 1931, are as follows: General form (of *Arthaberites alexandrae* Diener) similar to that of the Nevada species, except that the venter is broader in proportion to the height. Sutures do not overlap as much as on Nevada species but are similar. On flanks just below ventral shoulder are several points instead of one point, as on Nevada species. Then follows a saddle, a higher lobe, another saddle, and then the highest lobe as on Nevada species. Width of lobes greater in proportion to height than that of Nevada species.

A close resemblance is to another new species, *Perrinoceras novaditus*, which has an acute venter instead of a grooved venter and an adventitious lobe that either comes to a point or just begins to divide at the tip into two prongs.

Genus SAGECERAS Mojsisovics

Sageceras MOJSISOVICS, *1873*, p. 69; *1882*, p. 187; *1902*, p. 313; HYATT and SMITH, *1905*, p. 97; DIENER, *1917*, Ueber Ammoniten mit Adventivloben, p. 40; SPATH, *1934*, p. 57.

Type: *Goniatites Haidingeri* Hauer, 1846.
Geologic range: Anisic, Ladinic, Karnic.
Geographic range: Alpine-Mediterranean Himalayan, and East Pacific (Nevada) regions.

Spath characterizes the genus as follows:

> Sageceratidae having discoidal shells with small umbilicus and narrowly tabulate venter, which is bordered by keeled edges. Lines of growth sigmoidal. Suture-line ceratitic, with numerous adventitious and auxiliary elements.

One of the chief characteristics of the suture, which characterizes the genus, is the long, narrow parallel-sided lobes, with two points divided by a tiny saddle. The smaller auxiliary lobes are rounded instead of two-pointed.

Recognition of the genus is easy, but specific determination seems more difficult. Spath recognizes only two species, *S. walteri* Mojsisovics from the Anisian and Ladinian, and *S. haidingeri* Hauer, from the Karnian. Apparently the only differences aside from a separation on a stratigraphic basis, are that *S. haidingeri* sometimes has a spiral depression surrounding the umbilicus, which is wider than the umbilicus of *S. walteri*. Spath includes *S. gabbi* Mojsisovics, from Nevada (not California, p. 59) with *S. walteri*. Robert Schnetzer (1934, p. 72), following Simionescu (1913, p. 329, 364) and Welter (1915, p. 91), thinks that *S. walteri* and *S. haidingeri* cannot be separated. If this be true, we have united the three species into one. Horst Berndt (1934, p. 37) follows Renz (1911, p. 37) in considering *S. walteri* as a variety of *S. haidingeri*.

SAGECERAS cf. S. HAIDINGERI Hauer
Plate 60, figures 9, 10

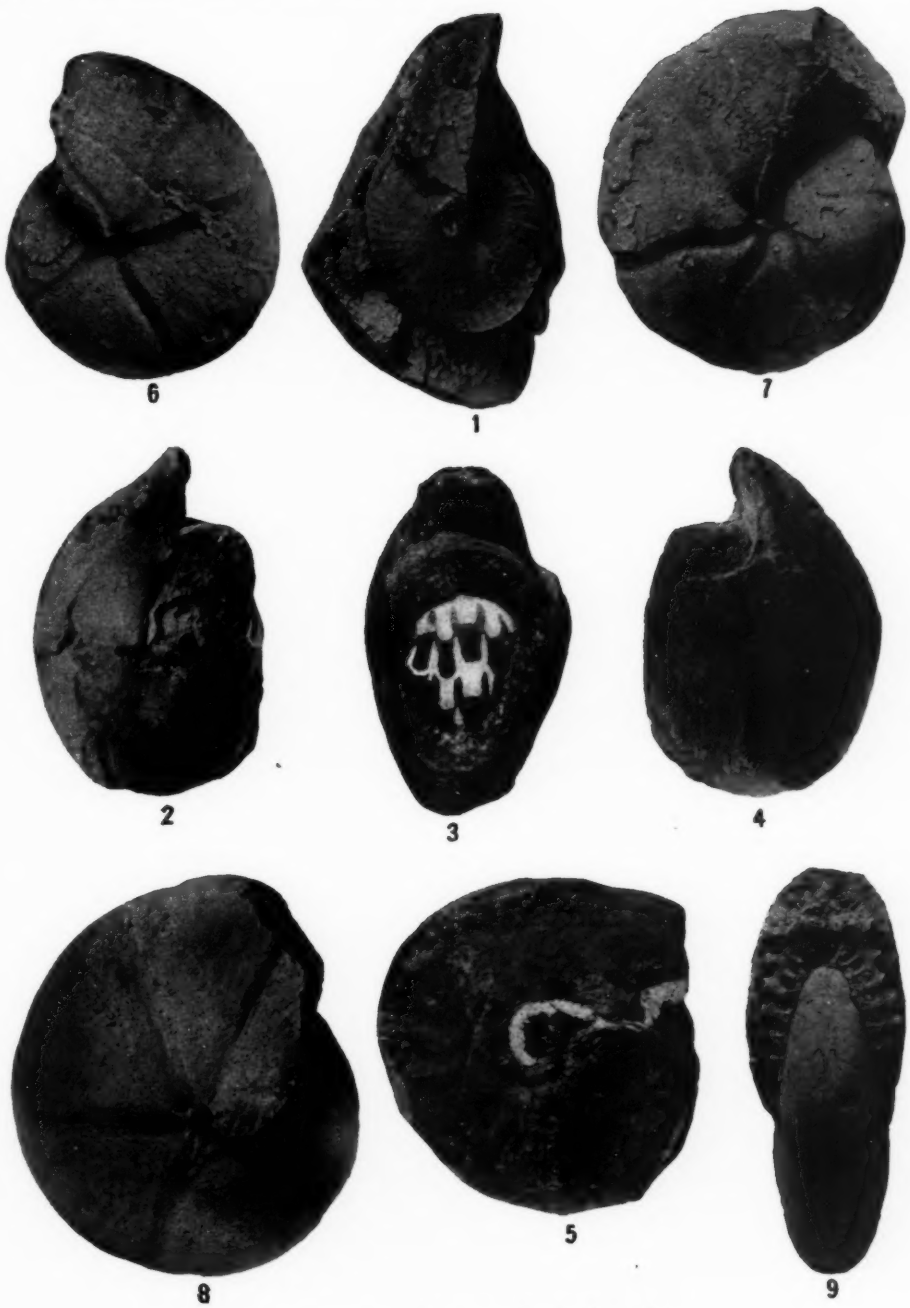
	D	H	W	U	H′	H/W
(1)	—	15	5	5	—	3.00
(2)	67	39	8.5	8	30.5	4.60
(3)	82	48	14	6.5	—	3.43

(1) *S.* cf. *S. haidingeri*, n. sp., pl. 60, figs. 9, 10.
(2) *S. haidingeri* Hauer, in Mojsisovics, 1873, p. 70.
(3) *S. gabbi* Mojsisovics, in Smith, 1914, pl. 21, figs. 18–20. The measurements are from Smith's original specimen.

Number of specimens studied, one frag-

EXPLANATION OF PLATE 62

FIGS. *1–5*—*Lobites* (*Lobites*) *gargantua* Johnston, n. sp. *1*, D=55 mm., showing radial sculpture on inner whorls. *2–4*, D=48 mm., type. *5*, D=50 mm. U. S. Nat. Mus. 77521. (p. 466)
6–9—*Joannites jacobus* Johnston, n. sp. *6*, D=46 mm. *7*, D=49 mm. *8*, *9*, D=56 mm. U. S. Nat. Mus. 77528. (p. 477)



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ment. This fragment shows the typical discoidal, compressed shape with almost flat, parallel sides and narrow umbilicus typical of the genus, along with the numerous characteristic bifid lobes. The shell, at the one spot on the venter where it is preserved, forms two faint keel ridges, one on each ventral shoulder. The ridges are absent on the internal mould, which is rounded over the venter.

The new specimen is wider in proportion to height than the two with which it is compared in the above table. There is no sign of a spiral depression bordering the umbilicus, such as is said to be typical of *Sageceras haidingeri* Hauer.

Genus LOBITES Mojsisovics

Lobites MOJSISOVICS, *1875*, p. 155; *1882*, p. 176; POMPECKJ, *1894*, p. 226; HAUG, *1894*, p. 390; MOJSISOVICS, *1902*, p. 286; RENZ, *1911*, p. 63; ARTHABER, *1914*, p. 159; *1927*, p. 114.

Type: *Clydonites ellipticus* Hauer, 1860.

Geographic range: Alpine-Mediterranean and Himalayan regions, Timor, Nevada, and British Columbia.

Geologic range: (Anisic?), Ladinic, Karnic.

Subgenera: *Lobites* s.s., *Paralobites*, *Psilolobites*, *Coroceras*, *Indolobites*.

This genus embraces globose forms with narrow umbilicus closed on the living chamber by a callus, which forms bear an outward resemblance to *Arcestes* but are characterized by (1) goniatitic sutures; saddle unserrated; lobes unserrated, single-pointed, except for *Indolobites;* or by (2) suture, or line, of evolution. This suture is formed on the living-chamber whorl between the callus which closes the umbilicus and the aperture. It follows a more or less regular spiral. It is not to be confused with the "sutures" formed by the junction of the camerae with the outer shell.

Halorites, a Noric genus, resembles the Karnic *Lobites* in general form and line of evolution of the living chamber, but the septa are ammonitic instead of goniatitic.

Lobites is divided into the following subgenera (see Renz, 1911, p. 63):

Lobites s.s. (Gruppe des *Lobites ellipticus* of Mojsisovics)—ribbed forms with simply pointed, unserrated lobes and rounded saddles. Type: *Clydonites ellipticus* Hauer (1860, p. 128, pl. 5, figs. 12–14). Range of subgenus: Alpine-Mediterranean Region, Himalayan Region; Peace River, B. C., and New Pass, Nevada. Ladinic-Karnic.

Paralobites Mojsisovics (1902) (Gruppe des *Lobites pisum* of Mojsisovics)—smooth-shelled forms with varices and rounded lobes and saddles. Type: *Goniatites pisum* Münster (1841, p. 127, pl. 14, fig. 6). Alpine and Himalayan region. Karnic.

Psilolobites Renz (Gruppe des *Lobites argolicus* of Renz, 1911)—smooth-shelled forms without varices, with simply pointed lobes and roundes saddles. Type: *Lobites argolicus* Renz (1911, p. 61; pl. 5, fig. 3; text fig.) Alpine-Mediterranean Region. Lower Karnic.

Coroceras Hyatt (see Meek, 1877, p. 107) (Gruppe des *Lobites monilis* of Mojsisovics)—sculpture and sutures as on *Lobites* s.s. but with "Kapuze" or double constrictions of the living chamber forming two hoods. Type: *Clydonites* or *Ammonites monilis* Laube (1869b, p. 64, pl. 37, fig. 4). Range: Alpine-Mediterranean, Himalayan, and West Pacific (Timor) regions, now found in Nevada. Karnic.

Indolobites Renz (1911). One specimen is known from the Himalayas, the only one in the world. Ribbed form with *serrated* lobes and rounded saddles. Doubtfully placed in the Middle Triassic although it

EXPLANATION OF FIGURE 2

A, *Metahedenstroemia? desertorum* Johnston, n. sp. Suture of pl. 61, fig. 4, ×2. (p. 460)

B, *Lobites* (*Lobites*) *carinatus* Johnston, n. sp. Sutures of pl. 61, fig. 6, ×3. (p. 466)

C, *Lobites* (*Coroceras*) *zephyrus* Johnston, n. sp. Sutures of pl. 61, figs. 11, 12, ×3, The type. (p. 468)

D, *Arcestes* (*Proarcestes?*) cf. *A.* (*P.*) *gaytani* Klipstein. Sutures from a fragment of H = 19 mm. ×2. (p. 474)

E, *Arcestes* (*Proarcestes?*), cf. *A.* (*P.*) *gaytani* Klipstein. Sutures from same fragment as above, ×2. (p. 474)

F, *Arcestes* (*Anisarcestes?*) sp. indet. Internal and umbilical sutures, ×5, of pl. 63, fig. 5. Dotted line on left indicates line of contact of outer whorl with inner whorl; dotted line on right indicates umbilical shoulder. (p. 474)

G, *Arcestes* (*Anisarcestes?*) sp. indet. External and umbilical sutures from same specimen as above. Dotted line represents umbilical shoulder. (p. 474)

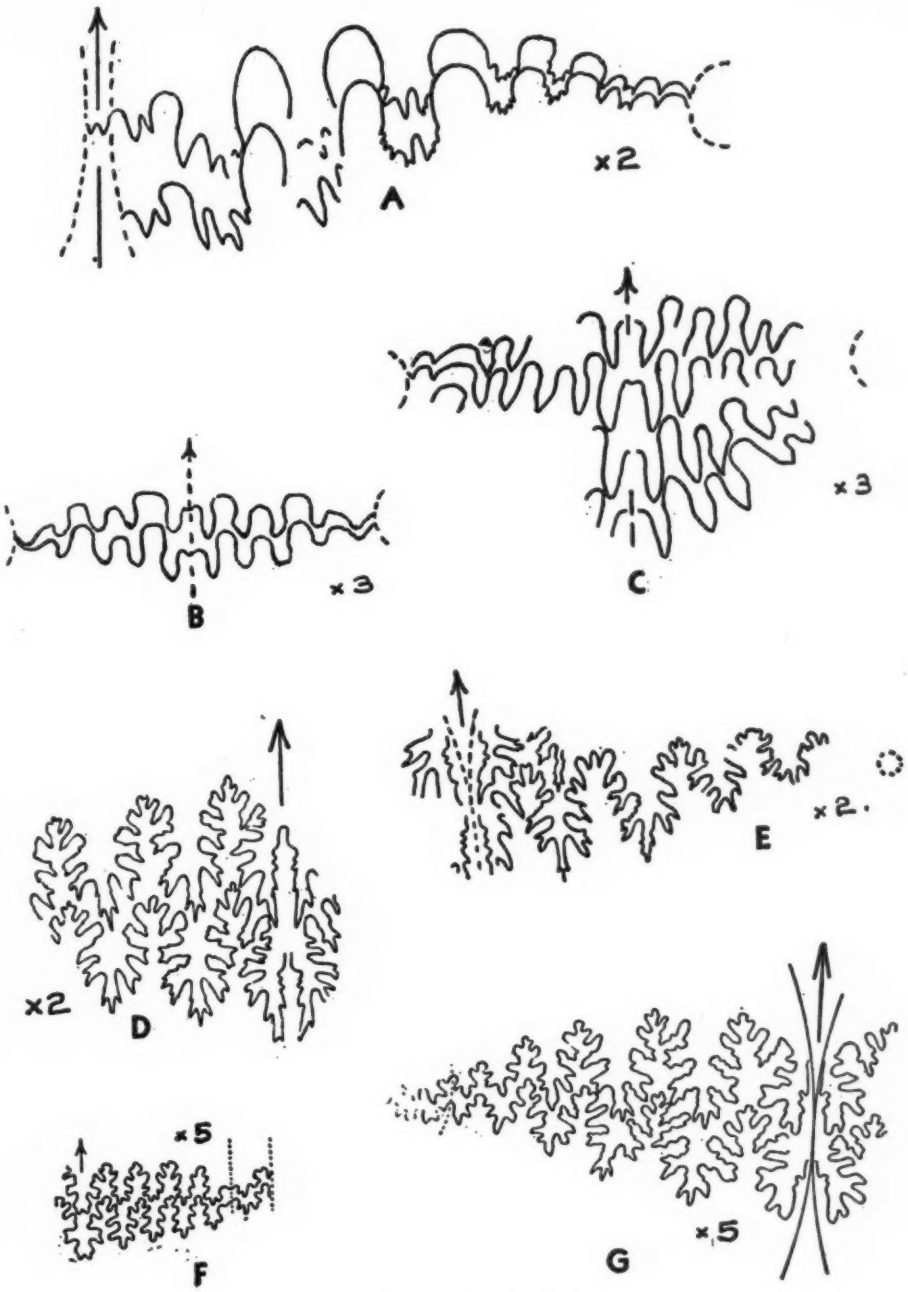


FIG. 2—Sutures of ammonites.

may be Upper Triassic. Type: *Clydonites oldhamianus* Stoliczka (1865, p. 50, pl. 4, fig. 4).

Of these groups *Lobites* s.s. and *Coroceras* have so far the most individual specimens and species, with *Paralobites* next.

Chambered kernels can be identified generically or possibly subgenerically by the sutures; but no specific determination is possible without the living chamber with, preferably, the aperture.

Aside from McLearn's description of a *Lobites* from the Peace River, British Columbia (1937, p. 96, pl. 1, fig. 15), the following new species present the first record of *Lobites* from North America.

LOBITES (LOBITES) CARINATUS
Johnston, n. sp.
Plate 61, figures 5–9; text figure 2B

	D	H/D	W/D	H/W
(1)	17.0	0.53	0.43	1.23
(2)	21.1	0.62	0.41	1.50
(3)	22.5	0.56	0.45	1.25
(4)	15.5	0.42	0.58	0.72
(5)	20.0	0.40	0.50	0.80

(1–3) *L. carinatus*, n. sp., pl. 61, fig. 5(1), fig. 6(2), figs. 7–9(3, type).
(4) *L. beneckei* Mojsisovics, 1875, p. 163, pl. 69, fig. 9.
(5) *L. schloenbachi* Mojsisovics, 1875, p. 164, pl. 69, fig. 6.

Number of specimens studied, eight.

The general shape is globose but somewhat compressed laterally. The umbilicus is closed at the beginning of the spiral of evolution of the living chamber but opens up along this spiral. At the last septum made by the animal, the venter is rounded and the radial ribs are either very faint or entirely lacking. The venter becomes more and more acute from this septum towards the aperture. The straight radial ribs, also becoming more pronounced orad, are paired on both sides. Each pair ends at a bead on the sharpened venter, giving the latter the appearance of having a keel, whence the name *carinatus*. These ribs begin at one-half whorl height and are not present nearer the umbilicus. Immediately before the aperture, the ribs die out, the beads disappear, and the venter again is rounded.

The suture of evolution appears to spring away from the umbilicus at about 45° to the radial ribs. The aperture forms an angle of about 135° with this suture. It has no lateral lappets but projects forward to a pronounced ventral lappet.

The living chamber is slightly more than one revolution long.

The sutures are goniatitic, with the lobes flame-pointed and the saddles rounded. Lobes are grouped in pairs of two by differences in the depths of the saddles. The first pair lies on the venter and is divided by the small saddle in the middle of the venter. The second pair lies on the flanks, the third pair near the umbilicus. The lobe nearest the umbilicus is very poorly developed.

The form resembling this new species most closely is *Lobites beneckei* Mojsisovics, which has a keel similar to our row of ventral beads, but weaker ribs. *L. schloenbachi* Mojsisovics is said to resemble it in having a sharp venter. All Nevada specimens are narrower in relation to diameter and whorl height than the European species.

LOBITES (LOBITES) GARGANTUA
Johnston, n. sp.
Plate 62, figures 1–5

	D	H/D	W/D	U/D	H/W
(1)	48	0.46	0.58	?	0.79
(2)	49.5	0.44	0.60	—	0.73
(3)	55	0.58	0.55	?	1.66
(4)	49	0.31	0.41	?	0.75
(5)	45	0.38	0.38	0.04	1.00
(6)	84	0.35	0.39	—	0.91
(7)	70	0.52	0.50	—	1.06
(8)	49	0.37	0.37	0.04	1.00

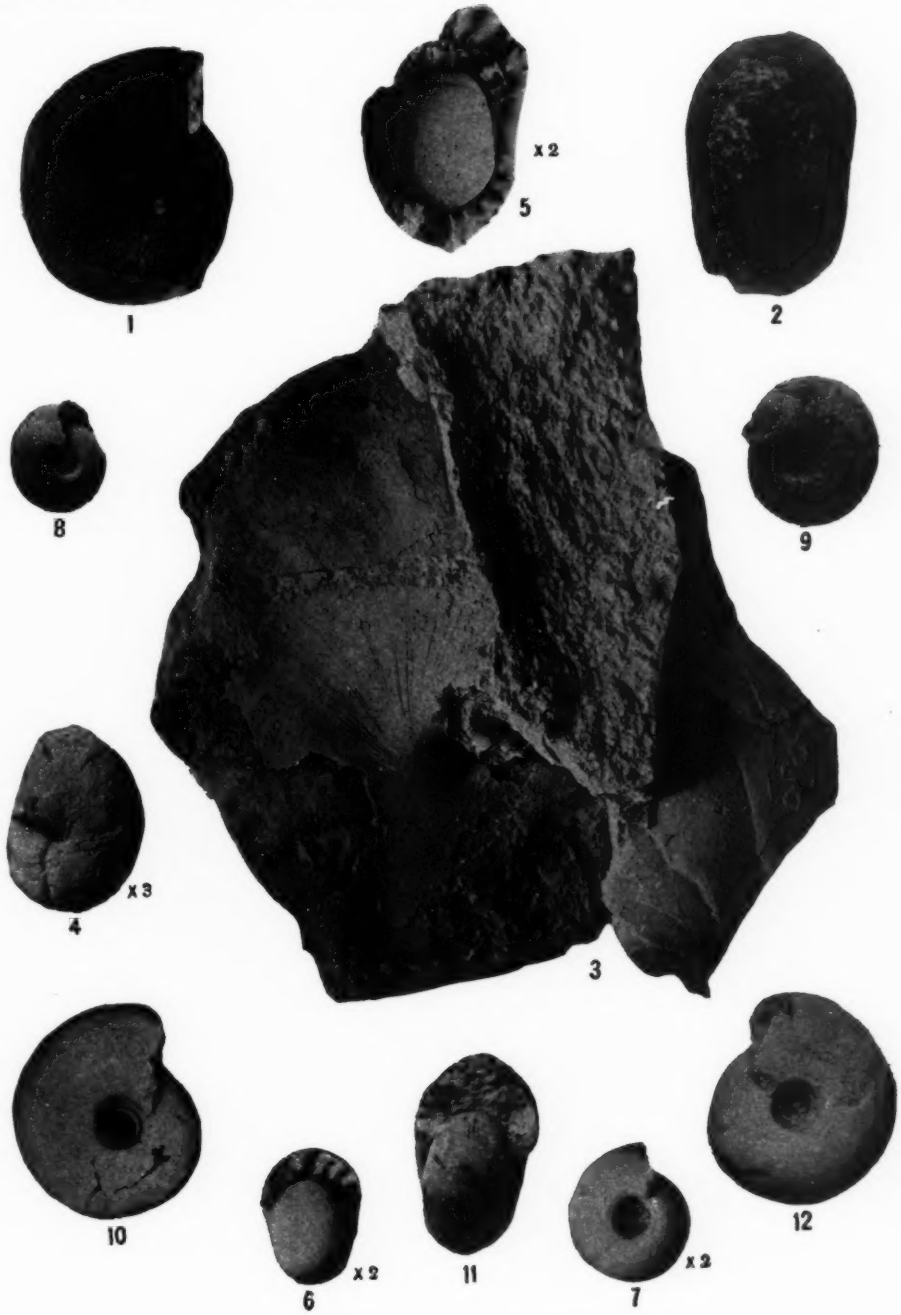
EXPLANATION OF PLATE 63

FIGS. *1, 2—Arcestes* (*Proarcestes?*) cf. *A.* (*P.*) *gaytani* Klipstein. D=37 mm. U. S. Nat. Mus. 77523. (p. 474)

3—Metahedenstroemia? desertorum Johnston, n. sp. D=88 mm. U. S. Nat. Mus. 77518. (p. 463)

4—Joannites jacobus Johnston, n. sp. D=8.2 mm., ×3. U. S. Nat. Mus. 77528. (p. 477)

5–12—Arcestes (*Anisarcestes?*) sp. indet. *6, 7*, D=9.5 mm., ×2. *5*, ×2, shows the inner kernel, *6, 7*, in the outer whorls. U. S. Nat. Mus. 77524. *8*, D=15.5 mm. U. S. Nat. Mus. 77525. *9*, D=20.8 mm. U. S. Nat. Mus. 77526. *10–12*, D=29.4 mm., type. U. S. Nat. Mus. 77524. (p. 474)



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(1–3) *L. gargantua*, n. sp., pl. 62, figs. 2–4(1, type), fig. 5(2), fig. 1(3).
(4–5) *L. ellipticus* var. *grandissima* Renz 1911, p. 59, pl. 5, fig. 6(4), fig. 4(5). The dimensions are from the illustrations.
(6–7) *L. euxinus* Kittl, after Simionescu, 1913, p. 55 (or p. 325).
(8) *L. philippi* Mojsisovics, 1902, p. 289.

Number of specimens studied, three.

The cross section is egg-shaped. The inner whorls are globose; the outer whorls with the living chamber are more compressed laterally, tapering to a less broadly rounded venter. The umbilicus is closed at the beginning of the living chamber. On the specimen of 55 mm. D an umbilicus 1.5 mm. wide was observed before the living chamber. The line or suture of evolution begins with the living chamber and opens up spirally. Lateral lappets not observed. The aperture turns inwards from both sides and seems bordered by a faint groove. The shell of the specimen of 48 mm. D is almost smooth but has faint radial folds becoming more pronounced and frequent away from the aperture. On the specimen of 55 mm. D at about the beginning of the living chamber, the narrow radial folds are quite pronounced and are separated by equally narrow furrows.

Sutures end about 1½ revolutions before the aperture. They are of the characteristic pattern of *Lobites* s.s.—ventral lobe divided by a saddle less deep than first lateral saddle; lobes pointed, saddles rounded; first and second lateral lobes divided by a saddle (second lateral saddle) less deep than third and first lateral saddles—they appear about like the divided ventral lobe; there is also another pair of lobes divided by a (fourth lateral) saddle smaller than the third; of this pair the third lateral is pointed and larger than the rounded fourth lateral lobe. One-half a small saddle terminates the visible part of the suture at the umbilicus. Internal suture unknown.

Aptycus, beaks, and soft parts of animal unknown.

Among known forms of comparable size, (1) *L. ellipticus* Hauer var. *grandissima* Renz (1911, p. 58, pl. 5, figs. 4, 6), is more compressed and with more pronounced radial ribs on the living chamber. Suture of evolution (pl. 5, fig. 4) is like suture on the internal mold of the Nevada species. (2) *L. euxinus* Kittl (figured also by Simionescu (1913), text figs. 50–52; pl. 5, fig. 1), which reaches about twice the size of any Nevada specimen, has inflated inner whorls similar to those of the latter. Width of mature specimens seems less in proportion to diameter than on Nevada specimens, ribs are stronger on the living chamber, and the aperture seems less pinched in at the sides than the one somewhat deformed example from Nevada on which the aperture is preserved. Lobes more irregular; one near umbilicus shows two points (fig. 52). (3) *L. phillipi* Mojsisovics (1902, p. 288; pl. 21, fig. 5) also is less wide in proportion to diameter, with flanks more nearly parallel, venter more acute. Suture of evolution two revolutions long compared with one revolution on Nevada species. Ornamentation similar.

This specific name is that of Rabelais' famous character, Gargantua, renowned for his unusual size.

LOBITES (COROCERAS) ZEPHYRUS
Johnston, n. sp.
Plate 61, figures 10–14; text figure 2c

	D	H	W	L[1]
(1)	23.0	15.5	13.0	31.2
(2)	31.1	18.0	11.5	37.4
(3)	29.5	20.0	16.0	38.3
(4)	—	—	11	31
(5)	—	15	16	42

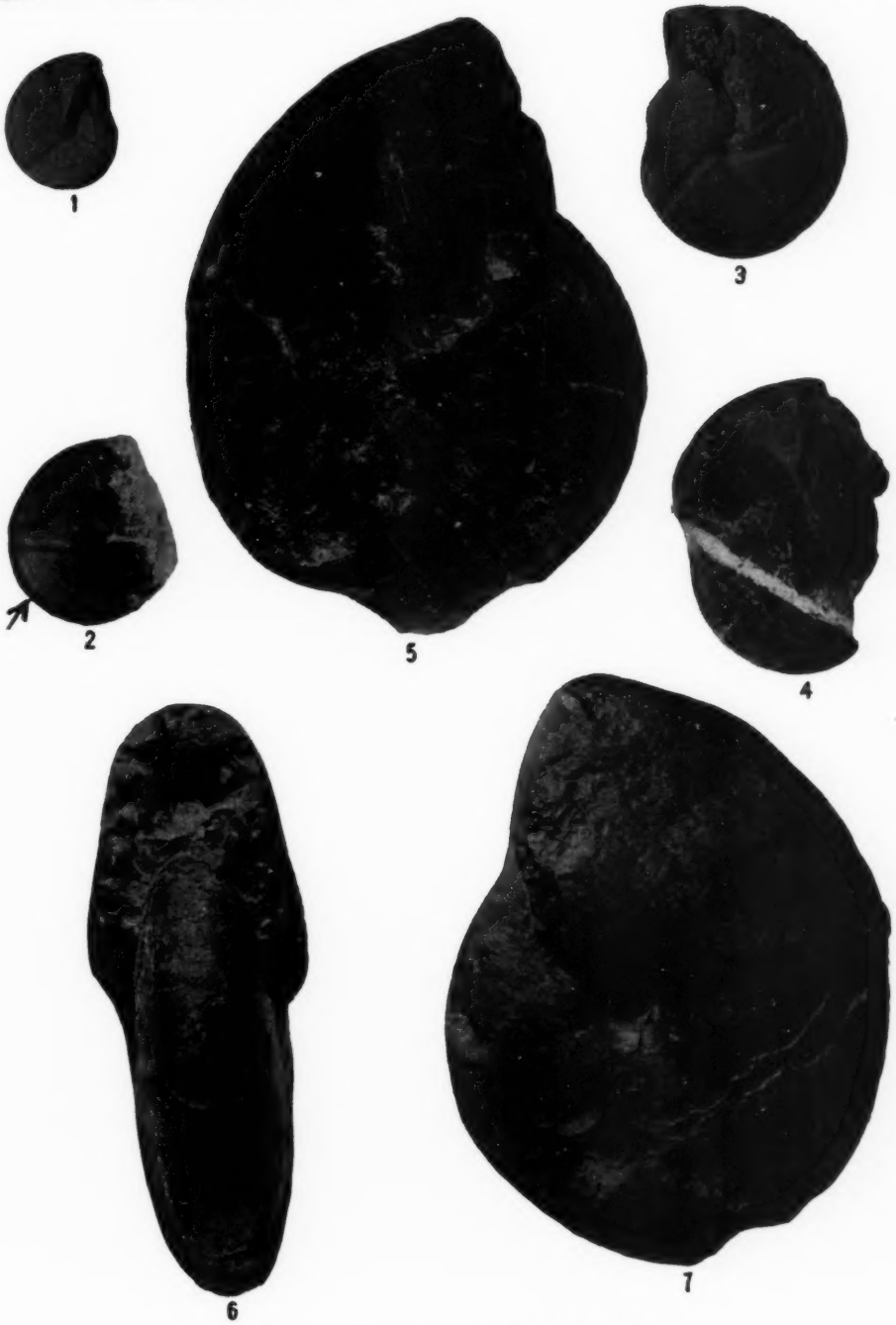
[1] L = maximum length. D and H are measured before the uncoiling that takes place in the living chamber.
(1–3) *C. zephyrus*, n. sp., pl. 61, figs. 11, 12(1), figs. 13, 14(2), fig. 10(3).
(4) *C. subnasutus* Mojsisovics, 1875, p. 171.
(5) *C. brouweri* Arthaber, 1927, pl. 17, fig. 2; measurements are taken from the plate.

Number of specimens studied, three.

Involute forms with whorls half as wide

EXPLANATION OF PLATE 64

FIGS. *1–7*—*Joannites jacobus* Johnston, n. sp. *1*, D = 19.1 mm. *2*, D = 26 mm.; arrow points to last septum or beginning of living chamber. *3*, D = 36.4 mm. *4*, D = 32.5 mm. *5–7*, D = 87.7 mm., type. U. S. Nat. Mus. 77528. (p. 477)



Johnston, Triassic Cephalopods

as the normal diameter. Typical of the subgenus *Coroceras* is the abnormal living chamber with an outer hood (German "Kaputze") caused by a constriction of the whorl about one-fifth revolution before the aperture, and a corresponding constriction on the whorl next inside forming the inner hood. The living chamber begins at the outer or inner edge of the inner constriction. The venter of the septate whorls appears rounded or flattened, but that of the living chamber is sharpened. Length of living chamber, about $1\frac{1}{4}$ revolutions.

Ornamentation: The living chamber is ornamented with faint to fairly strong radial ribs beginning at one-fifth whorl height and dying out on (faint ribs) or crossing (strong ribs) the venter. There are no ribs on the inner constriction or on the chambered part; none on the outer hood.

Septa: goniatitic, with six rounded lobes and six pointed saddles, like *Lobites* (*Lobites*) *gargantua*, n. sp. At not over 20 mm. whorl height, the third and fourth lateral lobes are more pronounced and are followed by a fifth and even a sixth (auxiliary) lobe. The first, third, and fifth saddles, being larger than the second, fourth, and sixth respectively, divide the lobes into sets of two, namely, first and second lobes, third and fourth, and fifth and sixth. The ventral lobe is divided by a saddle smaller than the first lateral saddle.

The aperture has a crimped edge.

The venter on the living chamber is more acute than on *L.* (*C.*) *subnastus* Mojsisovics, from the beds with *Lobites ellipticus* on the Röthelstein near Aussee, Austria. The related *L.* (*C.*) *brouweri* Arthaber from Timor has the flanks more pinched in at the aperture.

Genus Arcestes Suess

Arcestes Suess, *1865*, p. 76 (part); Laube, *1869b*, p. 86 (part); Mojsisovics, *1873*, p. 71 (part); *1882*, p. 153; *1893*, p. 783; *1896*, p. 79; *1899*, p. 95; *1902*, p. 261; Hyatt and Smith, *1905*, p. 73; Diener, *1919*, p. 2; Arthaber, *1927*, p. 44.

Type: Gruppe der *Arcestes galeati* Mojsisovics, 1873.

Geologic range: Anisic to Rhaetic.

Geographic range: World-wide.

The genus *Arcestes* in the widest sense includes smooth-shelled, globose or subglobose forms, very involute, with radial ridges on the inside (varices) causing constrictions on the internal mold, and occasionally radial folds (welts) or constrictions (labiae) on the outside of the shell. It is characterized by its suture, which is ammonitic, complexly subdivided, consisting of a divided ventral lobe, which is usually the largest of the lobes, and a series of lateral lobes decreasing gradually in size towards the umbilicus. The first lateral lobe may be larger than the ventral lobe. It has a general triangular form, as have also the lobes and saddles which succeed it. The peak of the lobes is at the base of the triangle of the saddles, and vice versa.

The genus is divided into the following subgenera:

1. *Arcestes* s.s. Includes the following divisions of Mojsisovics: "Gruppe der *Arcestes coloni*," "Gruppe der *A. intuslabiati*," and "Gruppe der *A. galeati*"). Type: Group of *Arcestes galeati*. Shape of living chamber differs from shape of inner chambered whorls; varices limited to latter whorls. Karnic to Rhaetic. World-wide. Abundant.

2. *Pararcestes*. Mojsisovics' "Gruppe der *Arcestes sublabiati*". Type: *Arcestes sublabiatus* Mojsisovics, 1875. Labiae and varices of the chambered whorls continue on the living-chamber whorls, which, however, differ from the former at least in the closing of the umbilicus by a callus. Diener points out (1919) that *A. colonus*, *A. bufo*, etc., placed by Mojsisovics under *Arcestes* s.s., have labiae or varices on the living chamber. Anisic, Karnic, (Ladinic?). Alpine-Mediterranean, Himalayan, and West-Pacific (Timor) regions. Abundant.

3. *Proarcestes*. See below. Abundant.

4. *Ptycharcestes*. Type: *Arcestes rugosus* Mojsisovics, 1893. Living chamber with fine radial ribs and apparently without labiae or

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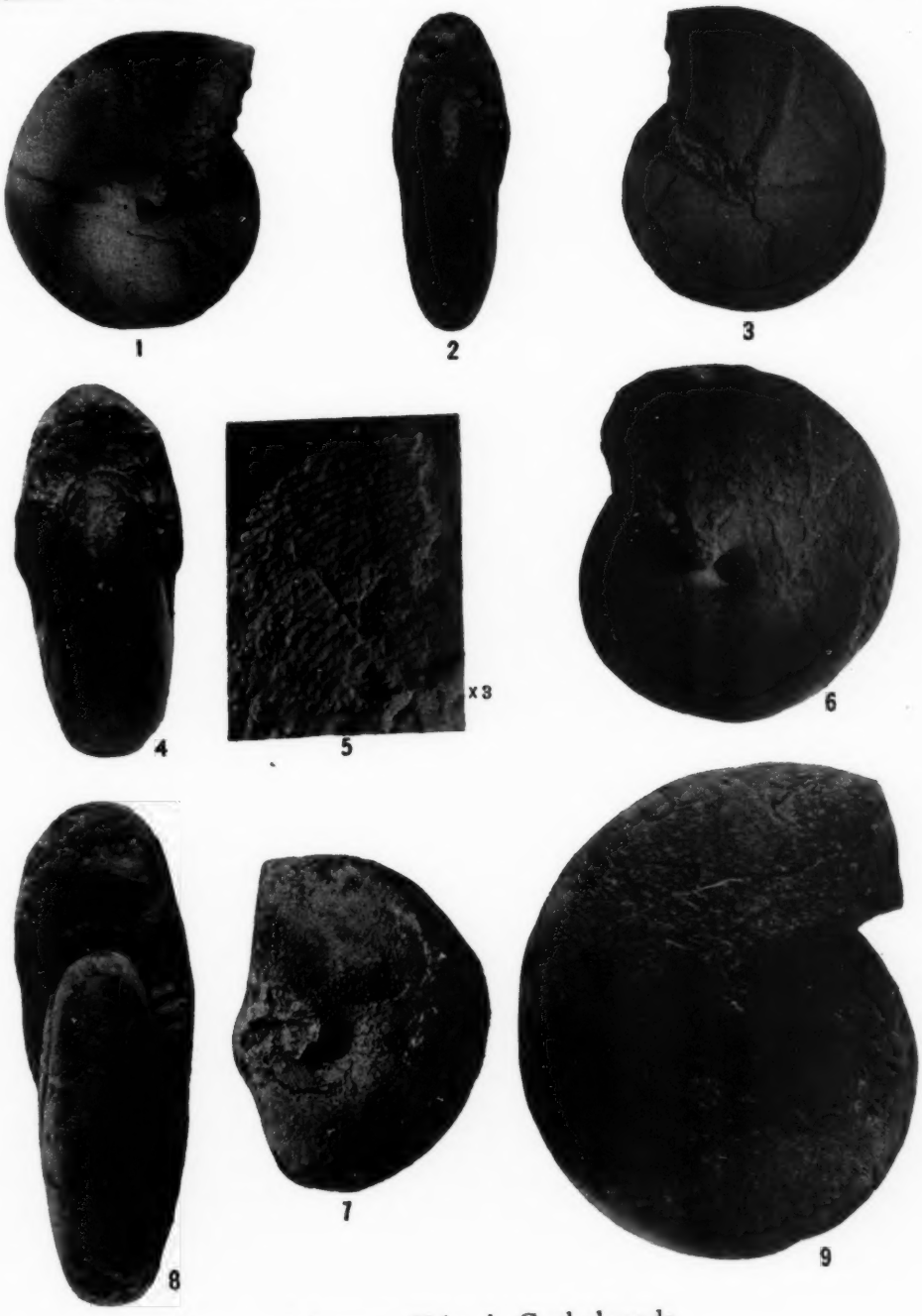
Explanation of Plate 65

Figs. *1–3*—*Joannites jacobus* Johnston, n. sp. D=43.2 mm., U. S. Mat. Mus. 77528. (p. 477)

4–7—*Procladiscites mulleri* Johnston, n. sp. *4–6*, D=50.5 mm., type. *5*, ×3, Enlarges the spiral lines. *7*, D=46.3 mm. U. S. Nat. Mus. 77530. (p. 480)

8, *9*—*Paracladiscites rogersi* Johnston, n. sp. D=71 mm., U. S. Nat. Mus. 77529. (p. 478)



Johnston, Triassic Cephalopods

varices. Inner whorls and sutures unknown. Karnic. Alps. Very rare—only two known specimens from which two species have been described.

5. *Stenarcestes*. Mojsisovics' "Gruppe der *Arcestes subumbilicati*," 1875. Type: *Ammonites subumbilicatus* (Bronn) Hauer, 1846. Discoidal arcestids resembling *Joannites* in shape, but with umbilicus deepened and usually surrounded by a spiral depression. Lobes numerous. Karnic, Noric. Alpine-Mediterranean, Himalyan, and West-Pacific (New Caledonia, and Timor) regions. Numerous species.

6. *Gonarcestes*. Type: *Arcestes piae* Diener 1919. Like *Arcestes* (*Pararcestes*) *genuflexus* Mojsisovics, this species has a bend in the living chamber, but the venter is contracted instead of expanded. Another contraction of the venter occurs at beginning of the living chamber. Alps. Karnic-Noric boundary. One known species.

7. *Anisarcestes*. Type: *Arcestes subdimidiatus* Kittl, 1908. Pararcestids with compressed outer whorls having labiae but with smooth globose inner whorls. A list of species included in this subgenus by Simionescu (1913, p. 357 or 87), with various criticisms, follows:

Arcestes dimidiatus Mojsisovics, to which Kittl (1908, p. 507) compares his type, is placed by the former under "Gruppe der *Arcestes intuslabiati*," hence under *Arcestes* s.s. Simionescu (1913, p. 358) says *A. subdimidiatus*, the type, has greater affinities with *A. perioclus* than with *A. dimidiatus*.

Arcestes subdimidiatus Kittl. The type. Placed by Kittl questionably under subgenus *Pararcestes*.

Arcestes perioclus Mojsisovics.

Arcestes conjugans Mojsisovics.

Arcestes pachystomus Mojsisovics. Diener (1919, p. 344) criticizes the placing in the subgenus *Anisarcestes* of this and of the above two species, assigned by their author to his "Gruppe der *Arcestes coloni*" and hence to *Arcestes* s.s. They all have a spiral depression about the umbilicus suggesting *Stenarcestes*.

Arcestes kittli Simionescu. With more acute venter than the type.

Arcestes mrazeci Simionescu. With flatter flanks, narrower venter than the type. No ornamentation to a diameter of 60 mm. except the "epidermides" (outer shell layer which is radially striated?)[1]

It is impossible to determine *Arcestes* subgenerically (and specifically) without having at least part of the living chamber preserved, unless the stratigraphic location is used to make guesses. For specific identification the aperture often is necessary, as Diener (1919, p. 342) and Arthaber (1927, p. 45) suggest. The latter gives an outline of the type of aperture (peristome) character-

[1] Spath, 1934, p. 42: "*epidermids* Minutely-branching or feltlike markings on surface of some smooth ammonites."

EXPLANATION OF TEXT FIGURE 3

A, *Joannites jacobus* Johnston, n. sp. Sutures, ×8, of pl. 63, fig. 4. (p. 477)

B, *Joannites jacobus* Johnston, n. sp. Sutures, ×8, of pl. 64, fig. 1. Dotted line represents umbilical shoulder; solid curved line represents contact of outer and inner whorls, called "suture of evolution," and divides external from internal sutures. (p. 477)

C, *Joannites jacobus* Johnston, n. sp. Sutures, ×3, of pl. 62, fig. 6. (p. 477)

D, *Joannites jacobus* Johnston, n. sp. Sutures, ×2, of pl. 69, fig. 6, fragment *a*, or pl. 70, fig. 1, fragment *a*. Dotted line *c* indicates suture of evolution: external sutures are to the left, internal to the right. Dotted line *b* indicates the umbilical shoulder. Dotted line *a* indicates suture of evolution of the next overlying whorl. (p. 477)

E, *Joannites jacobus* Johnston, n. sp. Internal sutures, ×2, of pl. 69, fig. 6, fragment *b*, or pl. 70, fig. 1, fragment *b*. Arrow indicates the dorsum and its antisiphonal lobe. (p. 477)

F, *Procladiscites mulleri* Johnston, n. sp. Sutures, ×3, from a specimen of 23.8 mm. diameter. (p. 480)

G, *Procladiscites mulleri* Johnston, n. sp. Sutures, ×2.5, of the type, pl. 65, figs. 4–6. (p. 480)

H, *Trachyceras* (*Trachyceras*) cf. *T. aonoides* Mojsisovics. Sutures, ×3.5, of a somewhat weathered specimen now lost. D=52.5 mm., H/D=0.57, W/D=0.38, U/D=0.17. Left dotted line represents suture of evolution; right dotted line, the umbilical shoulder. (p. 482)

I, *Trachyceras* (*Trachyceras*) cf. *T. aonoides* Mojsisovics. Sutures, ×2, of a smaller (less weathered) specimen, also lost. (p. 482)

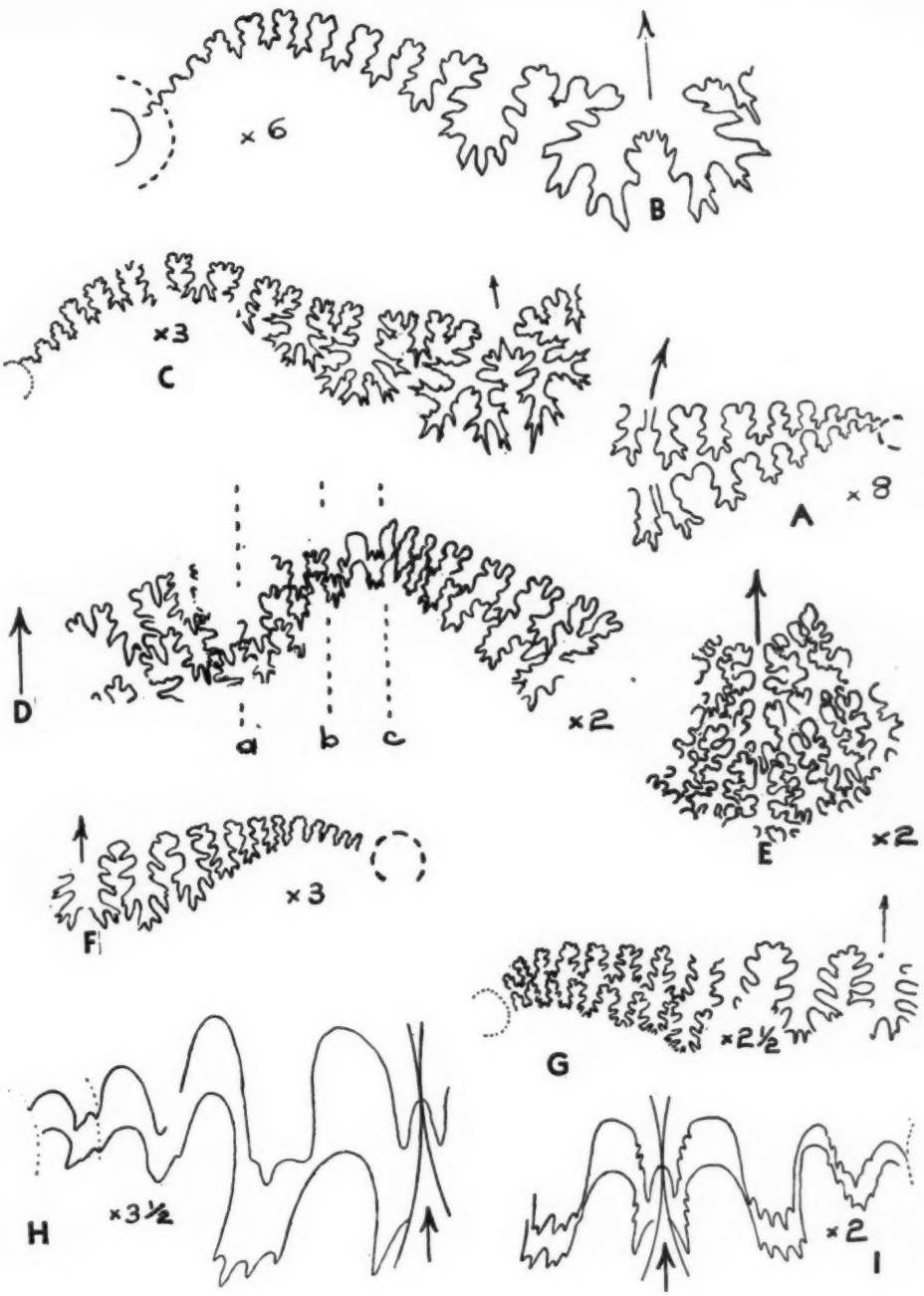


FIG. 3—Sutures of ammonites.

istic of each subgenus and "Gruppe" of the genus *Arcestes*.

Subgenus PROARCESTES Mojsisovics

Proarcestes MOJSISOVICS, *1893*, p. 785; HYATT and SMITH, *1905*, p. 74; DIENER, *1919*, p. 3 (p. 343); ARTHABER, *1927*, p. 49.

Type: *Arcestes bramantei* Mojsisovics (1869).

Geologic range: Anisic, Ladinic, Karnic.

Geographic range: Alpine-Mediterranean, Himalayan, East-Pacific (California, Nevada, etc.), and Arctic regions.

Proarcestes has a living chamber similar to the septate whorls in shape and in the presence of varices and labiae. The umbilicus is not even closed by a callus on the living-chamber whorl, as it is closed in some *Pararcestes*. This subgenus includes three of Mojsisovics' "groups," as follows:

1. Group of *Arcestes extralabiatus* has continuous radial folds on the living chamber, with exception of *A. marcoui* Mojsisovics, which has none.

2. Group of *Arcestes bramantei* does not have external welts accompanying the inner welts, as in the next group.

3. Group of *Arcestes bicarinati* has external and accompanying internal radial welts on the shell. *Arcestes gaytani* Klipstein, included in this group, does not show these features or has only two faint radial furrows on the internal mold (Mojsisovics, 1875, p. 100, pl. 58, figs. 1a and b).

This genus begins stratigraphically sooner than the others (Anisic).

ARCESTES (PROARCESTES) cf. A. (P.) GAYTANI Klipstein

Plate 63, figures 1, 2; text figure 2D, E

	D	H/D	W/D	U/D	H/W	H′/H
(1)	37	0.54	0.63	0.04	0.83	0.45
(2)	—	—	—	—	0.83	—
(3)	88	0.51	0.56	0.12	0.90	—
(4)	47	0.50	0.65	0.12	0.81	—
(5)	86	0.54	0.51	0.09	1.05	0.33

(1–2) *P.* cf. *P. gaytani*, pl. 63, figs. 1, 2(1); text figs. 2D, E(2).
(3–5) *P. gaytani* Klipstein: (3) in Mojsisovics, 1875, p. 100; (4) in Simionescu, 1913, p. 307; (5) in Diener, 1908, p. 18.

Number of specimens studied, three.

The general shape is semi-globose. Venter and sides are flattened, giving a rectangular cross section with rounded corners. The shell is very involute; the umbilicus is almost but not quite closed. The increase in height per revolution is over 120 per cent ($H'/H = 0.45$). There is no ornamentation; the shell is smooth. On each revolution there is a suggestion of at least two faint constrictions, which bend slightly forward on the venter. The living chamber is unknown, hence the species cannot with certainty be determined specifically. The sutures are those typical of the genus. The divided ventral is the largest of the lobes.

Although the species cannot be determined for lack of the living chamber, yet the specimens resemble closely the European species *gaytani* Klipstein in general form and sutures (see Mojsisovics, 1875, pl. 58, fig. 3 and Simionescu, 1913, text figure 25 on p. 307). The originals of Simionescu's plate 5, figure 6, text figure 25, and specimens labelled *A. gaytani* in the Heinrich collection in the Naturhistorischen Museum in Vienna were compared with the Nevada specimens. The European specimens all have a wider umbilicus in proportion to the diameter.

ARCESTES (ANISARCESTES?) sp. indet.

Plate 63, figures 5–12; text figures 2F, G

	D	H/D	W/D	U/D	H/W	H′/H
(1)	9.5	0.42	0.77	0.24	0.55	0.50
(2)	15.5	0.46	0.62	0.16	0.74	0.45
(3)	20.8	0.47	0.56	0.25	0.84	0.51
(4)	29.4	0.49	0.60	0.24	0.82	0.56
(5)	30	0.43	0.50	0.23	0.87	—
(6)	37	0.43	0.48	0.19	0.89	—
(7)	32	0.43	0.65	0.15	0.69	—

(1–4) *Anisarcestes?* sp. indet., pl. 63, figs. 6, 7(1), fig. 8(2), fig. 9(3), figs. 10–12(4).
(5–6) *A. mrazeci* Simionescu, 1913, p. 40.
(7) *A. subdimidiatus* Kittl (in Simionescu, 1913, p. 308).

Number of specimens studied, eight (also numerous small forms doubtfully assigned to this species.)

The general form is subglobose, with an open steep-sided umbilicus. The outer whorl is indented to half of its height by the inner whorl. The largest known specimen is not over 30 mm. in diameter. All whorls are completely septate: the living chamber is

unknown, hence the subgenus and the species are indeterminate. There is a gradation from the globose young stage (9.5 mm. D) towards the higher-whorled, more discoidal adults (29.4 mm. D). The shell is almost smooth. Near the umbilicus on specimens of 15.5 and 20.8 mm. D, it shows extremely fine radial striae (visible under the binoculars with the light parallel to the flanks), which may be equivalent to the growth striae of lesser relief on the specimen of 29.4 mm. D.

The sutures are typically arcestoid. They are known in detail only from the smallest specimen. The lobes decrease in size from the divided ventral lobe to the umbilical suture and increase in size from the umbilical suture to the dorsal lobe. The latter is undivided but two-pointed. There are five lobes between the ventral lobe and the umbilical shoulder, one lobe on the umbilical wall which differs in pattern from the others, four internal lateral lobes, and the dorsal lobe.

The largest Nevada specimen was compared with the originals of Simionescu's 1913 figures. *Arcestes* (*Anisarcestes*) *mrazeci*, of his plate 4, figure 6, is more discoidal, less globose than the former. The cross section of the whorls shows parallel sides and rounded venter, while the Nevada specimen shows sides arching towards the venter. Both have an open umbilicus. The shell of *A. mrazeci* has many closely spaced radial lines similar to those on the smaller Nevada specimens. The sutures are similar, but those of *A. mrazeci* are more finely branched, probably because drawn from a larger specimen.

Arcestes (*Anisarcestes*) *subdimidiatus* Kittl (in Simionescu, 1913, pl. 2, fig. 8) is more robust than *A. mrazeci* and hence similar to the Nevada species in this respect. There is a suggestion of one varix per whorl on the internal mold. There are fine radial striations as on *A. mrazeci*. These are not seen on the Nevada type. *A. subdimidiatus* has, on the living chamber, radial folds, which are strongest on the venter, dying out on the sides, two or three in a group, each group at intervals of about a quarter of a revolution of the whorl. These cannot be compared with anything similar on the Nevada specimens, as their living chambers are unknown, and none are as large (66 mm. D) as the Roumanian specimen showing these features.

Sphingites meyeri Klipstein (in Mojsisovics, 1875, p. 88, pl. 58, figs. 7, 8) shows some resemblance to the Nevada form in nature of the umbilicus and in general shape, but the whorls do not increase in height as rapidly as on the latter, and the umbilicus is wider. At 10–17 mm. D, U/D is 0.40–0.35 instead of 0.24–0.16.

Genus JOANNITES Mojsisovics

"Gruppe der *Arcestes cymbiformis*" MOJSISOVICS, *1875*, p. 83.

Joannites MOJSISOVICS, *1879*, p. 134; *1882*, p. 166; *1902*, p. 276; HYATT and SMITH, *1905*, p. 76; FRECH, *1907*, p. 21; ARTHABER, *1914*, p. 164; *1927*, p. 99.

Type: *Nautilus cymbiformis* Wulfen, 1793.

Geologic range: Anisic, Carnic.

Geographic range: Alpine-Mediterranean, Himalayan, and East-Pacific (Timor, etc.) regions; Nevada (new occurrence).

Subglobose, laterally compressed, very involute forms, with inner whorls almost completely covered by the outer. Surface smooth except for lines of growth. Inner kernel with some exceptions shows periodic radial constrictions or varices.

Trend of suture from venter to umbilicus curved, convex anteriorly. Ammonitic. Lobes decrease in size from the divided ventral lobe towards the umbilicus. Saddles generally divided into at least two parts by minor lobes between the major lobes. Living chamber said to be 1½ whorls long (only length of one whorl observed on Nevada specimens); shape of living-chamber whorl similar to that of chambered whorls.

The following list of characters may help in the separation of *Joannites* from other genera:

Joannites—Shell smooth; constrictions usually present; general trend of suture line curved, saddles bifid.

Romanites—Shell spirally striated; constrictions absent; trend of suture line strongly curved, saddles bifid.

Cladiscites—Shell spirally striated; constrictions absent; trend of suture line almost straight, saddles bifid.

Procladiscites—Shell spirally striated; constrictions absent; trend of suture line almost straight saddles not bifid.

Arcestes—Shell smooth; constrictions usually present; trend of suture line almost straight, saddles bifid.

Hyatt and Smith (1905, p. 76) described as "*Joannites*" *nevadanus* a species referred more correctly by Smith (1915, p. 44) to *Arcestes* (*Proarcestes*). The species which follow are the first known from North America having the true characteristics of *Joannites* namely: smooth outer shell, varices and constrictions, and bifid saddles.

The following lists are intended to be of help in the determination of species:

(1) Species with constrictions on outside of shell corresponding to varices inside of shell:

Joannites diffissus Mojsisovics.
salteri Mojsisovics.
subdiffissus Mojsisovics.
proavus Diener (1900, p. 13, pl. 1, figs. 1, 2).
macer Arthaber.

(2) Species without varices at diameters greater than 55 mm:

Joannites sp. indet. Mojsisovics, 1902, p. 276.
thanamensis Diener (1908 b, p. 47, pl. 7, fig. 1). This is one of the largest individuals of the genus, $D = 214$ mm. There are no furrows on the inner whorls but there is one near the aperture.
mojsvari Dienér (1909, p. 9, pl. 3, fig. 1).
sp. indet. Kittl, 1908, p. 505.
jacobus Johnston n. sp.

(3) Other species arranged according to number of varices at various diameters.

(a) Two varices per revolution:

Joannites joannis austriae Klipstein.
kossmati Diener (1908 a, p. 40, pl. 5, fig. 7). This is considered to be identical with *J. stefanescui* Kittl and with *J. joannis austriae* Klipstein var. *hellenica* Renz (1922, p. 240) although the latter have three varices per revolution.
cymbiformis Wulfen at $D = 240$ mm.
klipsteini Mojsisovics at $D = 8$ mm.
jacobus Johnston, n. sp., at $D = 8.2$ mm.

(b) Three varices per revolution:

Joannites cymbiformis Wulfen at diameters less than 90 mm., or greater than 126 mm. but less than 240 mm.
dieneri De Toni.
joannis austriae Klipstein var. *hellenica* Renz.
klipsteini Mojsisovics on next larger whorl than $D = 8$ mm.
stefanescui Kittl.
tridentinus Mojsisovics.
trilabiatus Mojsisovics (1882, p. 167, pl. 42, f. 2).
jacobus Johnston, n. sp. at 19.1 mm. D.

(c) Four to six varices per revolution:

Joannites caminensis Longhi. Six varices at 95 mm. D.
cymbiformis Wulfen. From 90 to 126 mm. D. there are four to five varices per revolution.
deranicus Arthaber. Five varices at 46 mm. D.
jacobus Johnston, n. sp. At 26 to 88 mm. D there are four to six varices per revolution of the whorl.
klipsteini Mojsisovics on whorls of 16 to 105 mm. D.
klipsteini Mojsisovics var. *compressus* Guggenberger, 1928. (The number of varices is not stated.)
klipsteini Mojsisovics var. *aegaeica* Renz.
klipsteini Mojsisovics var. *orientalis* Renz.
styriacus Mojsisovics.

(d) Seven varices per revolution.

Joannites klipsteini Mojsisovics var. *graeca* Renz, 1922, at 36 mm. D.

(e) Eight varices per revolution:

Joannites bathyolcus Boeckh.
klipsteini Mojsisovics var. *graeca* Renz, 1911. Specimen with living chamber.

(f) Twelve varices per revolution:

Joannites helenae Renz, 1922, at 60 mm. D.

Species arranged according to number of lateral lobes in the suture line.

EXPLANATION OF PLATE 66

FIGS. *1–4*—*Trachyceras* (*Trachyceras*) *desatoyense* Johnston, n. sp. *1*, Var., D=21 mm., U. S. Nat. Mus. 77533. *2*, Var., D=27 mm., ×2; U. S. Nat. Mus. 77534. *3*, D=43 mm. *4*, D=62 mm.; U. S. Nat. Mus. 77535. (p. 483, 484)

5–7—*Procladiscites mulleri* Johnston, n. sp. *5*, *7*, Enlargements, ×3, of the same specimen as shown in *6*, D=43 mm. U. S. Nat. Mus. 77530. (p. 480)

Johnston, Triassic Cephalopods

1

4

5

6 x 3

2

7

8

9

3

Johnston, Triassic Cephalopods

(a) Four and one-half lobes:
Joannites proavus.
(b) Five lobes:
Joannites cf. *J. salteri* (Mojsisovics) Arthaber, 1927, D 18 mm.
diffissus Hauer, D 15 mm.
kossmati Diener (*Traumatus* limestone, 1909), D 95 mm.
macer Arthaber, 1927, D 32 mm.
(c) Five and one-half lobes:
Joannites dieneri de Toni, D 64 mm.
(d) Six lobes:
Joannites joannis austriae Klipstein var. *hellenica* Renz.
caminensis Longhi, D 95 mm.
trilabiatus Mojsisovics, D 114 mm.
deranicus Arthaber, D 46 mm.
stefanescui Kittl (Simionescu, 1913, text fig. 33), D 50 mm.
alimanestoi Kittl = *stefanescui* = *kossmati* Diener, 1908.
kossmati Diener, D 67 mm.
(e) Seven lobes:
Joannites diffissus Hauer (Simionescu, 1913, text fig. 36, p. 47), D 46 mm.
cf. *cymbiformis* (Wulfen) Mojsisovics = *mojsvari* Diener, D 55 mm.
(f) Eight lobes:
Joannites joannis austriae Klipstein, D 182 mm. Mojsisovics: D 62 mm. Arthaber, 1927.
cymbiformis Wulfen. See Arthaber, 1927 p. 100, D 100 mm.; Diener, 1909, D 63 mm.
cf. *tridentinus* Mojsisovics (Diener, 1908, D 94 mm.).
klipsteini Mojsisovics (Diener, 1909, D 63 mm.; Arthaber, 1927, D 57 mm.).
helenae Renz, D 60 mm.
klipsteini var. *graeca* Renz, D 36 mm.
klipsteini var. *aegaeica* Renz, D 40 mm.
(g) Nine lobes:
Joannites klipsteini Mojsisovics, D 54 mm.
cymbiformis Wulfen, D 135 mm.?
thanamensis Diener, D 214 mm.
mojsvari Diener, D 178 mm. No varices.

JOANNITES JACOBUS
Johnston, n. sp.
Plate 62, figures 6–9; plate 63, figure 4; plate 64, figures 1–7; plate 65, figures 1–3; plate 69, figure 6; plate 70, figures 1, 2; plate 71, figures 1, 2; text figures 3 A–E

	D	H/D	W/D	H′/H	V[1]	L[2]
(1)	8.2	0.61	0.49	0.60	2	6
(2)	19.1	0.58	0.38	—	3	11
(3)	26.	0.58	0.38	—	4	10
(4)	32.5	0.58	0.40	—	?	10
(5)	36	0.55	—	—	4	11
(6)	43.2	0.57	0.37	0.46	5	11
(7)	46.0	0.56	0.34	0.55	5	10
(8)	49	0.57	0.36	—	6	—
(9)	56	0.57	0.39	0.36	6	—
(10)	87.7	—	—	—	5	10
(11)	117	0.53	0.44	0.44	0	10
(12)	128	0.56	—	—	0	10
(13)	94	0.52	0.33	—	6	—
(14)	62	—	—	—	—	9
(15)	44	0.57	0.48	—	5	—
(16)	64	0.52	0.42	—	6	—
(17)	—	—	—	—	—	8
(18)	56	—	—	—	6	8

[1] V = Varices per whorl.
[2] L = number of external lobes.

(1–12) *J. jacobus*, n. sp., pl. 62, fig. 6, text fig. 3C(7); fig. 7(8), figs. 8, 9(9: there are 11 internal lobes); pl. 63, fig. 4, text fig. 3A(1); pl. 64, fig. 1, text fig. 3B(2); fig. 2(3); fig. 3(5); fig. 4(4); figs. 5–7(10); pl. 65, figs. 1–3(6: there are 11 internal lobes); pl. 69, fig. 6, text fig. 3D(12); pl. 70, figs. 1, 2, text fig. 3E(12); pl. 71, figs. 1, 2(11). In (12), lobes were counted on the inner whorl, which still shows constrictions.

(13–18) *J. klipsteini* Mojsisovics, 1875, p. 84(13); pl. 61, fig. 3(14); in Diener, 1908b, p. 42(15); 1909, p. 8(16), pl. 2, figs. 1a, c(17). In (13), there are two varices per whorl at 8 mm. D, three on the next larger whorl, five to six at 62 to 105 mm. D. In (18), there are three varices per revolution of the whorl below 36 mm. D; four, five, or six varices between 35 and 55 mm. D.

Number of specimens studied, over 100.

The living chamber, as partially preserved on the specimens of 26 and 32.5 mm. D, attains a length of one-third and one revolu-

EXPLANATION OF PLATE 67

FIGS. *1–3*—*Trachyceras* (*Trachyceras*) cf. *T. aon* Münster. D = 69 mm. U. S. Nat. Mus. 77531. (p. 481)
4–6—*Trachyceras* (*Trachyceras*) *desatoyense* Johnston, n. sp. *4*, *5*, Type, D = 32 mm. *6*, Venter, ×3; D = 48 mm. U. S. Nat. Mus. 77535. (p. 483)
7–9—*Trachyceras* (*Trachyceras*) cf. *T. aonoides* Mojsisovics. *8*, *9*, D = 47.5 mm. U. S. Nat. Mus. 77532. (p. 482)

tion of the whorl respectively. All specimens show some shell, but only on that of 42.3 mm. D is it well enough preserved to show the radial striae of growth.

The umbilicus opens up from about 60 mm. D till 128 mm. D, the largest diameter known. It is not closed by a callus on even the most adult specimen.

The generic description applies well to this species. Its closest relative is *J. klipsteini* Mojsisovics. This was originally differentiated from *J. cymbiformis* Wulfen by its narrower form and more numerous varices. It was recognized that the number of varices varies with the diameter of the specimens. A comparison of the Nevada specimen of 43.2 mm. D with the original of Mojsisovics' (1875) plate 61, figure 3, showed that the latter, in addition to being larger (62 mm. D), was somewhat thicker in proportion to height. No actual measurements were made, unfortunately. It was noted that the Nevada specimen had 11 lobes including the ventral, the European 10 lobes; and that the illustration of the latter is the mirror image of the actual specimen.

Aside from these small differences, which may be only of varietal importance, the varices on the Nevada specimens at about 88 mm. D become very faint, disappearing entirely at a greater diameter, whereas on Mojsisovics' specimen of 105 mm. D (1875, pl. 61, fig. 2) the varices are shown very distinctly in the illustration.

The number of lateral lobes in the suture line increases from six at 8.2 mm. D to 10 or 11 at about 19 mm. D and thereafter remains constant.

The species is named in honor of the late Professor James Perrin Smith of Leland Stanford, Junior, University.

Genus CLADISCITES Mojsisovics
Subgenus PARACLADISCITES Mojsisovics

"Formenreihe des *Arcestes multilobatus*" MOJSISOVICS, *1873*, p. 80.
Paracladiscites MOJSISOVICS, *1896*, p. 657; *1899*, p. 103.

Type: *Ammonites multilobatus* Bronn, 1832.

Geologic range: Karnic, Noric.

Geographic range: Alpine-Mediterranean, Himalayan (including Timor), and Arctic provinces. Now found in Nevada.

Cladiscites includes forms with a suture like *Joannites* (lobes very serrated, saddles divided by minor lobes) but without varices or constrictions of any sort. *Paracladiscites* has a smooth shell, whereas *Cladiscites* s.s. (group of the *tornati*) and *Hypocladiscites* (group of the *subtornati*) both have spiral striae on the shell. The first is considered to have two lateral lobes (lobes above line of projection of the inner whorl on the outer) while the second and third have three lateral lobes each. *Paracladiscites* is first known in the beds with *Lobites ellipticus* (zone of *Trachyceras aonoides*).

PARACLADISCITES ROGERSI
Johnston, n. sp.
Plate 65, figures 8, 9

	D	H/D	W/D	U/D	H/W	H′/H
(1)	71	0.56	0.35	0.04	1.62	0.50
(2)	112	0.55	0.36	—	1.55	—

(1) *P. rogersi*, n. sp., pl. 65, figs. 8, 9.
(2) *P. gemmellaroi* Mojsisovics, 1902, p. 85.

Number of specimens studied, one entirely septate, two fragments.

The septate specimen is compressed discoidal with the umbilicus almost closed. The rounded umbilical shoulders overhang the umbilical suture (the line along which the outer whorl comes in contact with the inner whorl). The sides are flattened, also the venter, but the ventral shoulders are rounded. In cross section the whorls are widest near the umbilicus. They about double in height in one revolution.

Sutures are of the *Joannites-Cladiscites* type, as stated under the description of the genus. There are 10 lobes on the flanks and a divided ventral lobe, which alone occupies the venter.

The shell is smooth, without the spiral striae characteristic of *Cladiscites* and *Procladiscites*. There are no radial constrictions on the internal mold such as characterize *Joannites*. Except for this last feature, it looks like *Joannites jacobus*, n. sp. Closely resembling *P. rogersi*, n. sp., is *Paracladiscites gemmellaroi* Mojsisovics, although the latter has a living chamber which is widest near the venter, while the living chamber of the former is not yet known.

The new species is named in honor of

Professor Austin Flint Rogers of Leland Stanford, Junior, University.

Genus PROCLADISCITES Mojsisovics

Procladiscites MOJSISOVICS, *1882*, p. 171; ARTHABER, *1914*, p. 174.

Type: *Procladiscites brancoi* Mojsisovics, 1882.

Geologic range: Anisic, Ladinic.

Geographic range: Alpine-Mediterranean and Himalayan regions. Nevada.

According to Diener's catalogue (1915, p. 229) this genus includes the subgenera *Phyllocladiscites* Mojsisovics (1902, p. 279) and *Psilocladiscites* Mojsisovics (1896, p. 658), and, by inference, *Procladiscites* s.s. All these forms are discoidal, involute with the umbilicus barely open, without labiae or varices, and with an arcestoid type of suture having rounded saddles instead of the bifid saddles of *Cladiscites* and its subgenera.

Kittl (1908, p. 501) gives a table in which is summarized the distinguishing features and stratigraphic position of the *Cladiscitidea* and the *Joannitidae*. *Phyllocladiscites*, like *Procladiscites*, has spiral striae on the shell. The two are differentiated not on a morphologic basis but on a geographic basis. The first occurs in the Hallstatt or north Alpine region (Juvavic Provinz of Mojsisovics), the second in the Mediterranean or south Alpine region. *Phyllocladiscites* could well be eliminated.

Psilocladiscites, on the other hand, is well differentiated morphologically from *Procladiscites*. Its shell is smooth, without radial striations as in the latter; it has two lateral lobes instead of three.[1] Prior to 1940 there was only one species of *Psilocladiscites* namely *P. malaris* Hauer (1887, p. 30; pl. 4, fig. 3).

The following table should help in the separation of species of *Procladiscites* s.s. and of *Phyllocladiscites:*

	D	H/D	W/D	U/D	H/W
(1)	69	0.55	0.22	0.07	2.25
(2)	60	0.53	0.23	0.13	2.28
(3)	102	0.53	0.26	0.05	2.00
(4)	64	0.36	0.28	0.09	2.00
(5)	34	0.58	0.29	0.04	2.00
(6)	19	0.51	0.33	0.14	1.55
(7)	50	0.54	0.35	0.06	1.54
(8)	39	0.58	0.34	0.09	1.40
(9)	30.5	0.52	0.36	0.08	1.45
(10)	36	0.56	0.39	0.08	1.44
(11)	23.8	0.54	0.42	0.06	1.14
	50.5	0.58	0.48	0.07	1.34
(12)	21	0.60	0.55	0.07	1.09
(13)	35	0.53	0.56	—	0.95
(14)	15	0.54	0.66	—	0.82
(15)	29	0.55	0.69	—	0.80
(16)	33	0.52	0.69	—	0.75

(1) *P. brancoi* Mojsisovics: the genotype and the thinnest form.
(2) *P. yasoda* Diener.
(3) *P. arthaberi* Gugenberger.
(4) *P.* cf. *P. yasoda* (Diener) Welter, 1915, p. 112; pl. 91, figs. 4a–c.
(5) *P. pantanellii* Tommasi.
(6) *P. macilentus* Hauer.
(7) *P. griesbachi* Mojsisovics.
(8) Ditto, after Martelli, 1904, p. 95.
(9–10) *P. rodostoma* Tommasi.
(11) *P. mulleri*, n. sp., The figures represent the limits of variation for a number of specimens.
(12) *P. schlosseri* Reis.
(13) *P. connectens* Hauer.
(14) *P. crassus* Hauer, 1887, p. 31.
(15) Ditto, in Diener, 1900, p. 15.
(16) *P. proponticus* Toula, 1896, p. 170. This is the thickest form.

[1] This last distinction is of doubtful value. "Lateral lobes" lie between the venter and the line of involution, i.e., a line where a plane, at right angles to the diameter of an ammonite and lying on the venter of the inner whorl, cuts the outer whorl. Without using X-rays only one point on this "line of involution" is determinable—at the place where the outer whorl ends or is broken off. Hence on only one septum (chamber wall whose edge produces the suture line at its point of contact with the outer shell), as a rule, can the lateral lobes be determined. It is, in the first place, often impossible to determine this point because the end of the ammonite is crushed or otherwise damaged. Even when determined it is sometimes hard to say whether a particular lobe is lateral, adventitious (due to secondary subdivision of the ventral or of the first lateral lobe, or of the saddle between them), or auxiliary (dorsal to line of involution). In this paper, all lobes between the ventral lobe and the umbilical suture are considered as lateral lobes and are numbered 1, 2, 3, etc. (first, second, third, etc.), from the venter towards the umbilicus.

Incidentally, *Cladiscites martini* Smith (1927, p. 70, pl. 102, figs. 17–20) and *C. mendenhalli* Smith (1927, p. 70, pl. 102, figs. 21–24) do show the radial spiral sculpture characteristic of this genus (very faint on *C. martini*) but their sutures are more like those of *Procladiscites* than of *Cladiscites*, in spite of their assignment to the Karnic (bottom of the Upper Triassic) and not to the Anisic or Ladinic (Middle Trias). *Procladiscites* has hitherto not been known above the latter stages.

PROCLADISCITES MULLERI
Johnston, n. sp.
Plate 65, figures 4–7; plate 66, figures 5–7; text figures 3f, g

	D	H/D	W/D	U/D	H/W	H′/H
(1)	23.8	0.56	0.48	0.07	1.19	0.44
(2)	24.8	0.55	0.45	0.06	1.14	0.44
(3)	26.2	0.58	0.46	0.06	1.27	—
(4)	29.2	0.55	0.42	0.07	1.32	0.45
(5)	46.3	0.56	0.42	0.06	1.34	0.42
(6)	50.5	0.54	0.46	0.06	1.20	0.47

(1–6) *P. mulleri*, n. sp., text fig. 3f (1, with 11 lateral lobes); pl. 65, fig. 7(5, with 11 external lateral lobes and 11 internal lateral lobes), figs. 4–6, text fig. 3g(6, with over 9 lateral lobes).

Number of specimens studied, 13.

Involute, discoidal forms, usually with spiral striations and arcestoid sutures. The saddles are rounded instead of bifid as on *Cladiscites*, *Joannites*, or *Romanites*. Height of whorls greater than width by one-fifth to one-third. Umbilicus almost closed, but distinct. Living chamber at least one revolution long. Eleven internal and 11 external lateral lobes, plus the divided ventral and the undivided dorsal lobe, at a diameter of 46.3 mm. Whorls increase in height somewhat less than 50 per cent per revolution.

In the Geologischen Reichsanstalt in Vienna were sought the originals of Mojsisovics, 1882, plate 48, figures 3, 4. Three specimens were found, none of which appeared to be the original of figure 3. All were badly preserved and seemed thinner in proportion to diameter than the Nevada species. According to Mojsisovics this species has a flattened venter with abrupt ventral shoulders, but the Nevada species shows only a rounded venter with rounded shoulders: the gradation from sides to venter is not abrupt.

P. (*Phyllocladiscites*) *rodostoma* Tommasi (1899, p. 31, pl. 4, fig. 4; pl. 5, fig. 1, text fig. 3) seems to be near to the Nevada species both in proportions and in rounding of the ventral shoulders. It also has 11 lateral lobes. The chief apparent difference is a slightly lesser width in proportion to height of whorl and to diameter.

P. schlosseri Reis (1901, p. 88; pl. 4, figs. 18, 19) at 21 mm. D is a slightly more robust form than the Nevada species. It also seems to have a rather rounded venter without sharp ventral shoulders.

This species is named in honor of Dr. Siemon William Muller of Leland Stanford, Junior, University, Palo Alto, California, who collected the type and many of the specimens here described.

Genus TRACHYCERAS Laube

Trachyceras LAUBE, *1869a*, p. 7; MOJSISOVICS, *1879*, p. 140; *1882* (part), p. 93; *1893*, p. 617; HAUG, *1894*, p. 405; FRECH, *1903* (or *1911*), p. 21; SMITH, *1904*, p. 387; HYATT and SMITH, *1905*, p. 191; SMITH, *1914*, p. 127.
Protrachyceras TORNQUIST, *1898*, p. 659.
Trachyceras und *Protrachyceras* ARTHABER, *1914*, p. 131.

Type: *Ceratites aon* Münster (1834, p. 13, pl. 1, figs. 4, 5; pl. 2, fig. 6.

This genus includes as subgenera:

Trachyceras s.s. Ladinic to Karnic. Alpine-Mediterranean, Himalayan, and Arctic regions. Now for the first time described from North America.

Protrachyceras Mojsisovics, 1893. Anisic?, Ladinic, and Karnic. Alpine-Mediterranean, Himalayan, American, and Arctic provinces.

Anolcites Mojsisovics, 1893. Anisic, Ladinic, and Karnic. Alpine-Mediterranean, Himalayan, American, Arctic, and Western Pacific regions.

Paratrachyceras Arthaber, 1914. Anisic and Karnic. Alpine-Mediterranean, and Himalayan provinces; North America.

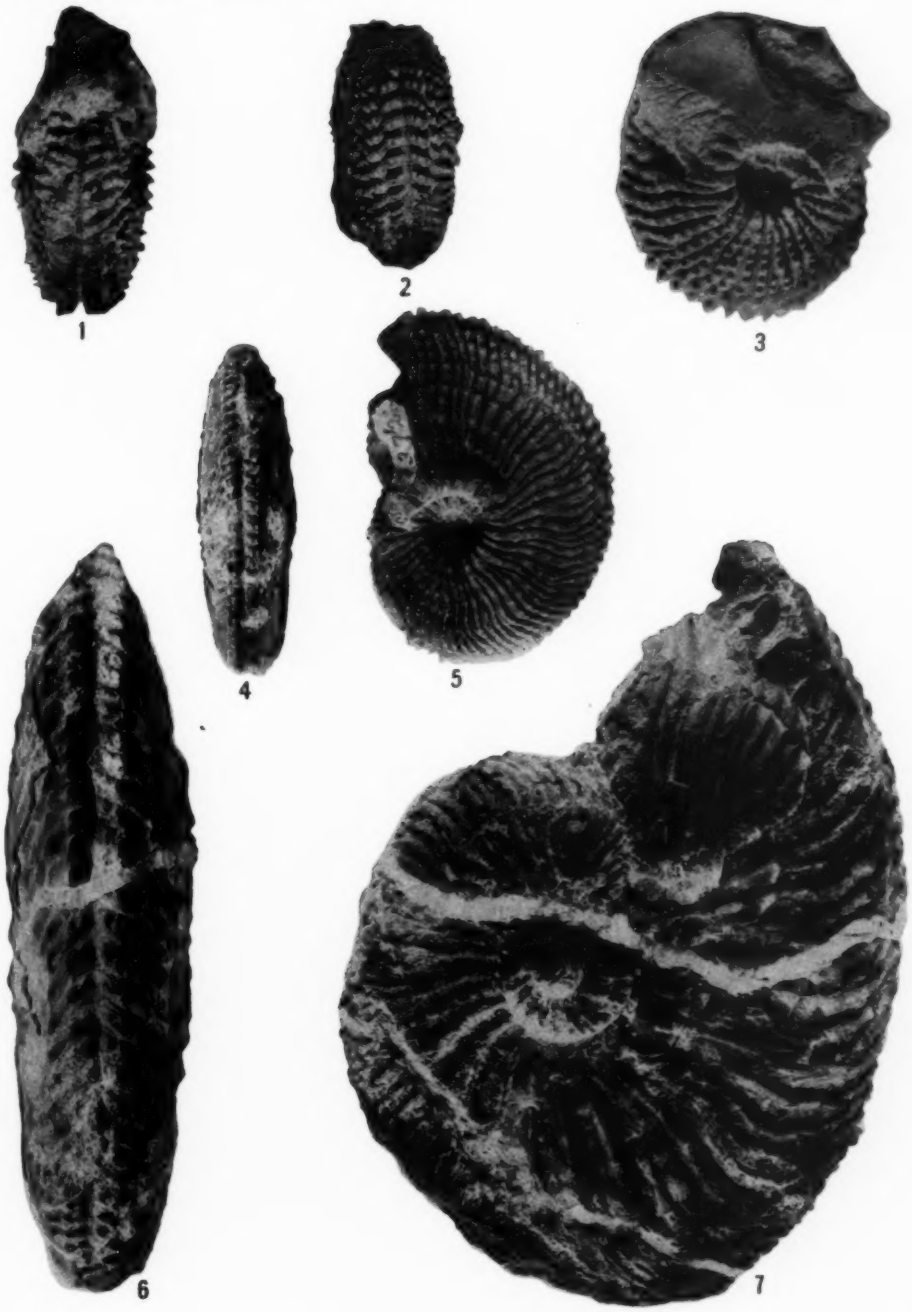
A translation of Laube's original description of the genus follows:

Shell more or less discoidal, strongly involute, with narrow rather deep umbilicus. Aperture higher than wide; edge of the aperture projected into a blunt ventral lappet; living chamber somewhat more than half of the last whorl. Suture line: siphonal saddle blunt, tongue-shaped. Siphonal

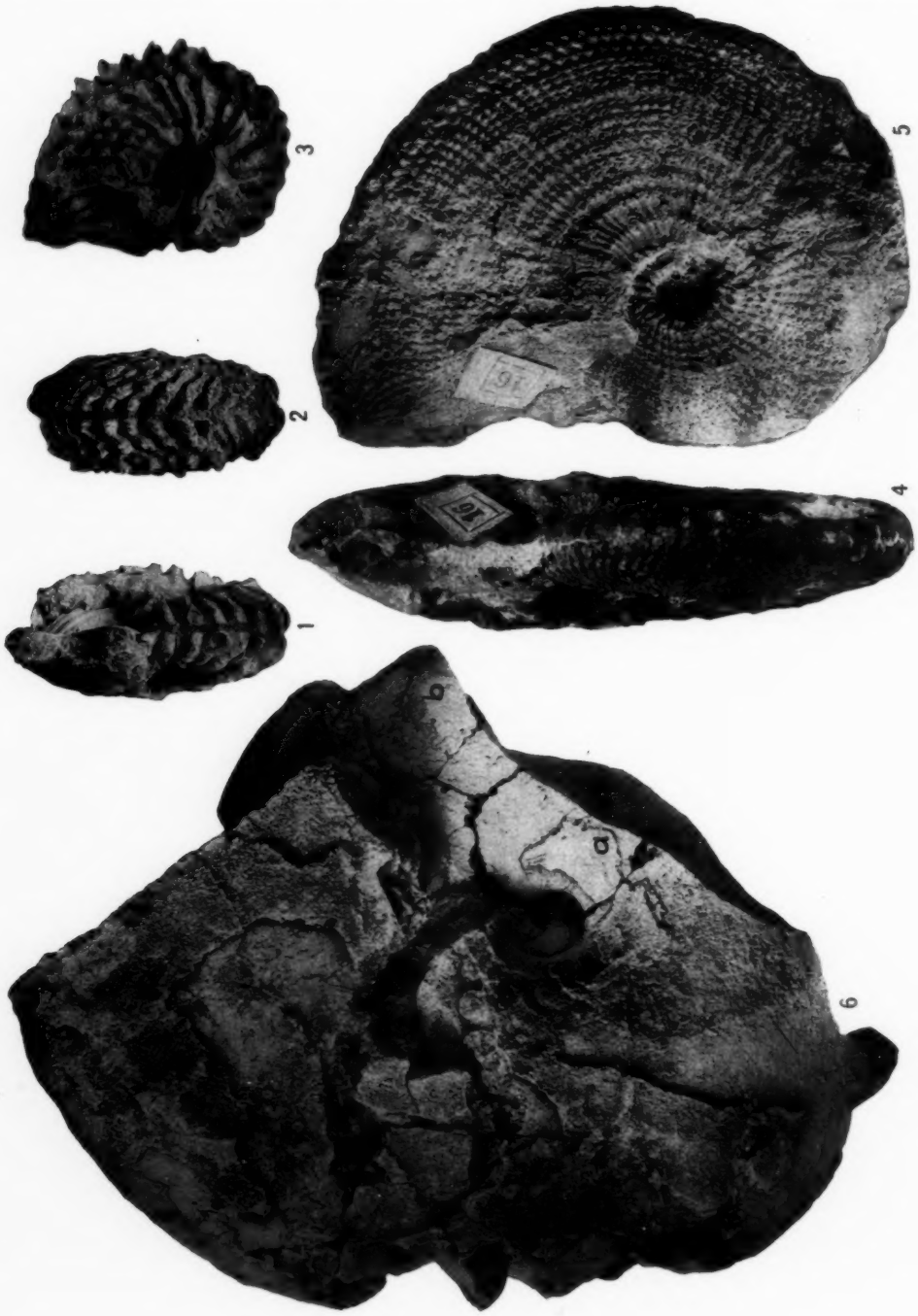
EXPLANATION OF PLATE 68

FIGS. *1–3*—*Trachyceras* (*Trachyceras*) *trispinosum* Johnston, n. sp.; holotype. U. S. Nat. Mus. 77538. (p. 488)

4–7—*Trachyceras* (*Trachyceras*) *desatoyense* Johnston, n. sp. *4*, *5*, D=48 mm., U. S. Nat. Mus. *77535*, *6*, *7*, Var. *compressum* D=16 mm.; U. S. Nat. Mus. 77536. (p. 483, 484)



Johnston, Triassic Cephalopods



Johnston, Triassic Cephalopods

lobe short, five-pointed; first lateral saddle blunt, with crenulated sides; principal lobe five-fingered, deep and broad, the deepest point directed diagonally from the middle towards the second lateral saddle. The following lateral saddles and lateral lobes similar in relationships to the principal lobe and the first lateral saddle. Venter with a smooth furrow, which is ornamented on both sides with knots with several parts. Sides flat, beset with closely packed, sickle-shaped, rough-knotted ribs. The spines follow one another in exact spiral lines agreeing in size and appearance.

The genus *Trachyceras* is limited to the Trias. The type of the same is *Trachyceras aon* Münster sp. from St. Cassian.

Mojsisovics in 1893 made three subdivisions of the genus: (1) *Trachyceras* s.s. with a row of double-pointed spines bordering the ventral furrow on both sides, (2) *Protrachyceras*, with single-pointed spines either side of the ventral furrow, and (3) *Anolcites*, with a weak ventral furrow crossed without a break by the radial ribs. Arthaber further separated as the subgenus *Paratrachyceras* finely-ribbed forms with not more than one or two spirals of spines on the umbilical or marginal edge, forms which otherwise resemble *Trachyceras*.

Clionites, members of which were originally included in *Trachyceras*, is distinguished by a more open umbiliçus and whorls increasing less rapidly in height. Furthermore, typical *Clionites* near C. *angulosus* Mojsisovics in form have no spirals of spines on the flanks. It is only forms from the top of the Karnic or higher beds, similar to J. P. Smith's subgenera of *Clionites*, which are strongly nodose or spinose. The *Clionites* from lower horizons are less highly ornamented, limiting spines or knots generally to an umbilical and a ventral spiral.

No *Trachyceras* s.s. has yet been described from North America. There is, however, no doubt that the forms here described from New Pass belong to this category, as the double-pointed ventral spines were exposed after laborious cleaning.

There are so many *Trachyceras* in the Karnic beds at New Pass that this was at first called the *Trachyceras* zone but on second thought changed to *Joannites* zone in order not to cause confusion with J. P. Smith's *Trachyceras* subzone of the zone of *Tropites subbullatus*. The New Pass zone is definitely lower and older. None of the *Trachyceras* resemble those from the *Trachyceras* subzone of California. The California forms have all been placed in the subgenus *Protrachyceras* because they lack the double-pointed spiral of spines bordering the ventral furrow. Their sutures are decidedly ammonitic, with serrated saddles. Their sculpture is generally more subdued than on the Nevada forms, both the true *Trachyceras* from New Pass and the *Protrachyceras* from the Middle Trias of the West Humboldt Range.

Probably more species are present than are here described. Poor preservation and difficulties of cleaning such highly ornamented forms have prevented further determination. About 200 specimens belonging to the genus were collected, more than any other genus, *Joannites* included.

TRACHYCERAS (TRACHYCERAS)
cf. T. AON Münster
Plate 67, figures 1–3

	D	H/D	W/D	U/D	H/W
(1)	69	0.51	0.29	0.16	1.75
(2)	83.5	0.53	0.25	0.14	2.10

(1) *T.* cf. *T. aon* Münster, pl. 67, figs. 1–3: type. The living chamber is one-half revolution long; most of the shell is preserved; and there are 16 spirals of spines.

(2) U. S. National Museum No. 3181 from Aussee, Austria. Acquired from the K. k. geol. Reichsanstalt and labeled "*Ammonites aon*," but it is more likely *Trachyceras aonoides* var. *fissinodosa*. There are 22 spirals of spines.

Number of specimens studied, one.

The type is discoidal, narrowly umbilicate, with whorls increasing rapidly in height and with U-shaped cross section. The

EXPLANATION OF PLATE 69

FIGS. *1–3*—*Trachyceras* (*Trachyceras*) *bispinosum* Johnston, n. sp. Holotype; D=40 mm., U. S. Nat. Mus. 77537. (p. 487)

4, 5—*Trachyceras* (*Trachyceras*) *aonoides* var. *fissinodosa* Mojsisovics. U. S. Nat. Mus. 3181, from Aussee, Austria. Acquired from the K. k. geol. Reichsanstalt and originally labelled "*Ammonites aon*." (p. 482)

6—*Joannites jacobus* Johnston, n. sp. D=ca. 128 mm., type. U. S. Nat. Mus. 77528. (p. 477)

umbilicus, though narrow, is open, so that the inner whorls may be seen. Its walls are steep, slightly arched, so that the suture where the outer whorl is in contact with the inner is overhung. Umbilical shoulders are abruptly rounded, surmounted by projections on the ribs with small spines. Lines in continuation of these ribs slope diagonally forward on the umbilical walls.

The flanks, as usual in this genus, are ornamented with falcoidal radial ribs surmounted by spirals of spines. There are 14 spirals, counting twice the double-pointed spines next to the ventral furrow. The ribs are not as fine and dense as on *Trachyceras* cf. *T. aonoides*. *Trachyceras aon* Münster has 12–14 spirals of spines. As Mojsisovics pointed out (1893), in the Raibl beds there are forms with 14–17 spirals of spines intermediate between *T. aon* and *T. aonoides* with 17–25 spirals. Hence *T. aon* and *T. aonoides* may be one and the same species.

The height is much greater in proportion to width on the Nevada species than on any of the European species.

The sides are very gently arched, with greatest width at the umbilical shoulders. The venter itself includes only the double-pointed spirals of spines and the ventral furrow. The latter is deeply incised, appearing distinctly on the internal mold as well as on the outside of the shell. Sutures unknown.

This form is extremely similar to some of the forms classed with *T. desatoyense* and may merely be a variety of the latter. It has more spirals of knots at similar diameters and finer, more numerous ribs on the septate whorls.

TRACHYCERAS (TRACHYCERAS)
cf. T. AONOIDES
Mojsisovics

Plate 67, figures 7–9; text figures 3H, I

	D	H/D	W/D	U/D	H/W
(1)	28	0.54	0.39	0.20	1.36
(2)	36	0.49	0.26	0.19	1.88
(3)	44.6	0.56	0.36	0.18	1.56
(4)	47.5	0.55	0.35	0.17	1.57
(5)	49	0.55	0.35	0.18	1.56
(6)	50.0	0.55	0.33	0.16	1.70
(7)	94	0.53	0.32	0.14	1.66

(1–6) *T.* cf. *T. aonoides* Mojsisovics. Pl. 67, figs. 8, 9(4), is the type: H′/H is .81.
(7) *T. aonoides* Mojsisovics, 1893, p. 696.

Number of specimens studied, more than 6.

This species probably resembles *Trachyceras aonoides* Mojsisovics more closely than any other species, showing particular affinity to the variety *fissinodosa* Mojsisovics (this paper, pl. 69, figs. 4, 5) with very fine, closely spaced sculpture of numerous ribs and spirals of spines. It is hard to differentiate the European and Nevada specimens with only Mojsisovics' illustrations to go by, which represent larger specimens than any known from Nevada. Sutures of the Nevada specimens seem less ammonitic, with entire, unserrated saddles.

At first the Nevada forms were thought to resemble *Trachyceras aon* Münster. Sculpture of the latter, however, is coarser, and there are differences in form. Comparison with the originals of Mojsisovics, 1882, plate 21, figures 15, 17 showed the Alpine species to be wider in proportion to diameter than the Nevada species. His figure 18 has almost the same proportions as the Nevada species, but the specimen had been compressed.

Simionescu's *Trachyceras aon* (1913, pl. 3, fig. 1) also seemed much wider in proportion to height than the Nevada specimens.

The general shape is discoidal, laterally compressed, with narrow but open umbilicus, and whorls increasing rapidly in height (2.5 times per revolution). Outer whorl embraces one-half of the inner and is indented by the inner to one-fifth of whorl height. The cross section of the whorl forms a narrow V with rounded apex. Umbilical shoulders abrupt, umbilical walls vertical.

The ornamentation consists of the usual falcoidal radial ribs with spiral rows of knots, interrupted on the venter by a distinct furrow that is noticeable even on the internal mold. It is the nature of the ornamentation that, in combination with the narrow umbilicus and rapid growth in height of the whorl, distinguishes this species from related species. The ribs and spines are extremely fine and close together. On the type are at least 20 spirals of spines at less than 26 mm. whorl height. Forward-sloping lines continue the ribs on the umbilical

walls. As usual, there is a double spiral of spines beside the ventral furrow.

The living chamber is about half a whorl long. The aperture seems to have a sinuous trend, following the trend of the ribs. Sutures are of the usual *Trachyceras* type. Saddles do not seem to be serrated. The divided ventral lobe has a few serrations. The broad, serrated, first lateral lobe is the largest of all. The second lobe comes to a point with serrations on the sides. There is a still smaller lobe on the umbilical wall, the umbilical shoulder, or on the flanks just outside of the shoulder. The internal lateral lobe must be larger than the latter. The dorsal lobe apparently is undivided, fairly large.

None of the young stages are similar to the broad, rough-shelled *münsteri* and *brotheus* stages described by Mojsisovics for *T. aon*. On the contrary, they already resemble the adult in form and ornamentation at 20 mm. D. At lesser diameters the width is greater in relation to height of whorl, but the sculpture always remains fine. One specimen of a diameter of 28 mm. before the living chamber shows at least three revolutions of the whorls before the central protoconchial whorl of less than 1 mm. D. Towards the protoconch the whorls constantly diminish more rapidly in height than in width, so that the innermost whorls are wider than high.

TRACHYCERAS (TRACHYCERAS)
DESATOYENSE
Johnston, n. sp.
Plate 66, figures 3, 4; plate 67, figures 4–6; plate 68, figures 4–7

	D	H/D	W/D	U/D	H/W	S[1]
(1)	32	0.50	0.28	0.19	1.78	11
(2)	43	0.53	0.28	0.17	1.87	11
(3)	48	0.54	0.29	0.17	1.86	11
(4)	57	—	—	—	—	11
(5)	62	0.49	0.21	0.21	1.60	10
(6)	72	—	—	—	—	10
(7)	51	0.43	0.29	0.23	1.40	15
(8)	72	0.44	0.33	0.27	1.33	11
(9)	72	0.49	0.27	0.19	1.80	13

[1] S = number of spirals of spines on each side, counting the double-pointed ventral spines as two spirals.

(1–6) *T. desatoyense*, n.sp., pl. 66, fig. 3(2); fig. 4(5); pl. 67, fig. 6, and pl. 68, figs. 4, 5(3); pl. 67, figs. 4, 5(1, the type, having part of the aperture. Living chamber is over one-half revolution long).

(7) *T. felix* Mojsisovics, 1893, p. 651, pl. 175, figs. 2a, b: a form similar to the above but with more spirals of spines.

(8) *T. fortunae* Mojsisovics, 1893, p. 652, pl. 175, fig. 5: This form is similar to the new species in number of spirals of spines but not in shape. The umbilicus is wider and the whorls are wider in proportion to height and diameter.

(9) *T. januarius* Mojsisovics, 1893, p. 687, pl. 193, figs. 1, 2. Fig. 2 is like the new species in form but has two more spirals of spines. It belongs in Mojsisovics' *margaritosa* group.

Number of specimens studied, eight.

The general shape is discoidal, laterally compressed. The umbilicus is open but small. The umbilical walls are vertical or overhanging, and the umbilical shoulders are abruptly rounded. The greatest width of whorl is across these shoulders. Sides almost flat but gently arched, grading into the venter. This is occupied only by the two spirals of double-pointed spines and the furrow between them. This furrow is not deeply incised. It does not sink far below the level of the intercostal furrows but is chiefly accentuated by the double-pointed spines which end the radial ribs.

The shells are ornamented by the above-mentioned radial ribs bearing spines arranged in spiral rows. The ribs are falcoidal, bending slightly backwards in the middle of the flanks, then forward at about three-fourths whorl height. These ribs are fine, rather dense, and separated by intercostal spaces about as wide as the ribs are wide. The density of the ribs varies from specimen to specimen and even on the same specimen. Ribs are particularly fine and dense immediately before the aperture. The nature of the ribs is also very varied. Occasionally a rib runs straight from the umbilicus to the venter without forking. More often two ribs start at an umbilical spine. There may be further forking on the flanks, up to the fifth spiral of spines. A fork itself may be forked. Intercalations of ribs also are quite numerous. The details of the ribbing are complex.

The spines are very small, no higher above the ribs than the ribs above the intercostal spaces. As a rule there are nine spirals of spines plus the double-pointed spiral bordering the ventral furrow—11 spirals in all. The two largest specimens, however, seem to have only 10 spirals. The usual spine is rounded, but the points of the double-pointed ventral spines are elongated radially.

These are the largest, most prominent spines.

On the specimen of 48 mm. D there are 22 spines in a revolution at the umbilical shoulders and about 67 spines per revolution on the venter—about three times as many. As each spine is on a rib, these figures give some idea of the increase in number of ribs, by forking or intercalation, from the umbilicus to the venter. This same specimen shows that the outer whorl embraces about three-fourths of the inner whorl, and that it is indented to one-fifth its height by the inner. The height of the whorl increases five times in a revolution—a rapid growth.

Suture line unknown.

The above forms probably belong in Mojsisovic's "Gruppe der *Trachycerata margaritosa*" which includes *Trachyceras aon*, the type of the genus, and *T. aonoides*. Both of these have more numerous spirals of spines (14–25) but *T. januarius* has only two more spirals of spines at 72 mm. D than the Nevada specimens. Members of other groups, although bearing at maturity some resemblance to our new species, have more robust young forms with accentuated marginal spines—features that none of the Nevada specimens show.

TRACHYCERAS (TRACHYCERAS) DESATOYENSE Johnston, var.
Plate 66, figures 1, 2

	D	H/D	W/D	U/D	H/W
(1)	27	0.52	0.33	0.22	1.56
(2)	21	0.48	0.29	0.24	1.67

(1–2) *T. desatoyense* Johnston, var., pl. 66, fig. 2(1), fig. 1(2).

Number of specimens studied, two.

The larger of these two specimens has the general shape of the type of *Trachyceras desatoyense* but lacks its spines on the flanks. In suitable light, suggestions of spirals of spines on the flanks can be made out. Clearly visible are the double-pointed ventral spiral, two spirals close together on the ventral shoulder, and a fifth spiral somewhat lower. There are three extremely weak spirals on the flanks, and two stronger ones next to the umbilicus. Total spirals, 10.

Ribs are more widely spaced than on the type but are still fine. The larger specimen shows a pathological condition near the aperture. Here the ribs digress from normal. Two major ribs join on the ventral shoulder, entirely enclosing an intercalated rib on the flanks.

The living chamber is at least one-half whorl long.

The septae are clearly visible on the larger specimen. These are of the usual *Trachyceras* type. The ventral lobe cannot be seen, as this part of the specimen is broken off. The first lateral is the largest and broadest lobe. It has three points. The next lobe is smaller and comes to a point. There should be a third smaller lobe just on the umbilical shoulder. Saddles are perhaps crenulate but not serrate.

The smaller specimen also shows the living chamber. Here the lateral spirals are even fainter than on the larger specimen, perhaps nonexistent.

TRACHYCERAS (TRACHYCERAS) DESATOYENSE var. COMPRESSUM Johnston, n. var.
Plate 68, figures 6, 7

	D	H/D	W/D	U/D	H/W	S[1]
(1)	45	0.51	0.33	0.24	1.35	10
(2)	116	0.50	0.25	0.21	1.38	10

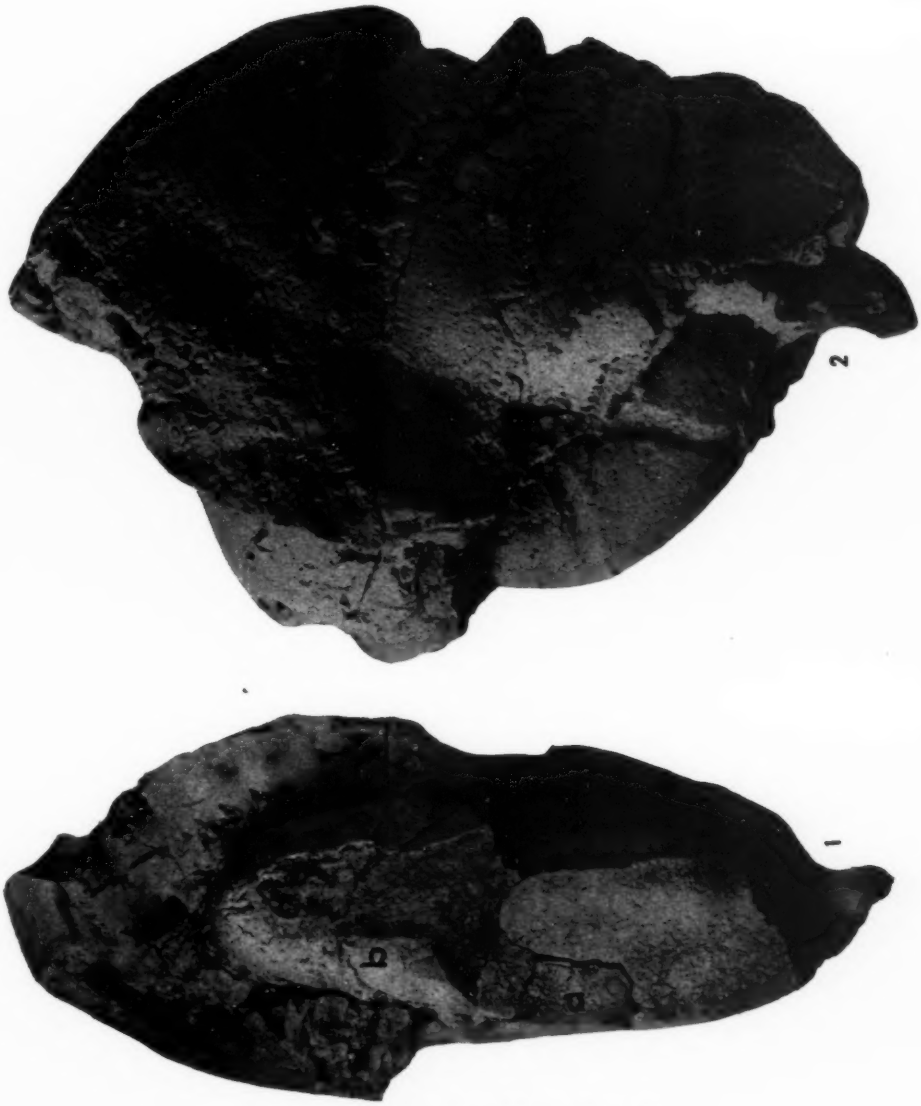
[1] S = number of spirals of spines on a side.

(1–2) *T. desatoyense* var. *compressum*, n. var., pl. 68, figs. 6, 7(2, veined and somewhat distorted type).

Number of specimens studied, three.

This variety is taken to include forms more widely umbilicate and more compressed than the average with nine or 10 spirals of small spines (seven or eight spirals plus the double-pointed ventral spiral). Unfortunately, each of the three specimens included in the species is veined with calcite, and the largest specimen is also somewhat distorted.

This specimen of about 116 mm. D may be considered as the type. The aperture is not present. At least the last half of the last whorl represents a living chamber. At the assumed beginning of this living chamber the ribs seem broader and coarser than usual but become finer forwards. The ventral furrow is very faintly incised at the beginning of the last whorl but more strongly at the end, where it falls below the level of the intercostal spaces.



Johnston, Triassic Cephalopods

FIGS. *1, 2*—*Joannites jacobus* Johnston, n. sp. Type, D = ca. 128 mm. U. S. Nat. Mus. 77528. Note the strong radial constrictions on the inner whorls of *2* which do not appear on the outer whorls. (p. 477)

Johnston, Triassic Cephalopods

FIGS. *1, 2*—*Joannites jacobus* Johnston, n. sp. D=117 mm. U. S. Nat. Mus. 77528. (p. 477)

The compression, considered the varietal characteristic, may be secondary due to crushing and may not represent an original character of the shell.

TRACHYCERAS (TRACHYCERAS) BISPINOSUM Johnston, n. sp.
Plate 69, figures 1–3

	D	H/D	W/D	U/D	H/W
(1)	30	0.47	0.47	0.25	1.00
(2)	40	0.50	0.45	0.24	1.11
(3)	90	0.50	—	0.20	—

(1–3) *T. bispinosum*, n. sp., pl. 69, figs. 1–3(2, type). The other two specimens are internal molds. (3) is septate.

Number of specimens studied, nine.

This is a robust, coarsely ribbed, very spiny form. The long spines are hardly ever preserved. Instead, on the internal mold, one sees the coarse ribs with periodic nodes, which, next to the ventral furrow, give the species the appearance of a *Protrachyceras*. When, however, the spines can be separated from the enclosing rock matrix, the ventral row is seen to have the double points characteristic of *Trachyceras* in the strict sense.

On the type the height of whorl is greater than the width. If, however, the umbilical spines had been completely preserved, the width probably would exceed the height. On one side of the type are visible the bases of these spines, with tips broken off, on the other side are only the nodes on the internal mold which underlie the spines. Greatest width of whorl lies across the umbilical shoulders on which these spines originate.

The ornamentation is complex. No intercalated ribs seem to exist. The coarse ribs curve forward from the umbilicus to the venter and are surmounted by the spines already mentioned. In one spiral, though there is some variation in size of spines, all are approximately of one size. But from spiral to spiral are pronounced differences in size. At 20 mm. whorl height (H) are eight spirals of spines, or 11 according to Mojsisovic's way of counting as the fifth, seventh, and eighth are double-pointed. These latter, plus the umbilical spiral of which the tips are missing, are the spirals of large spines. Spirals 2, 3, 4, and 6 are small, single-pointed. The ribs start at the umbilicus singly or in twos or threes, forking from a knot. The greater the number of ribs to which it gives rise, the larger the knot or spine. At the fifth spiral, ribs may fork again. One case of forking at the seventh spiral was also observed. There is no forking at the smaller spines.

The ventral furrow is very pronounced, rectangular. It sinks below the level of the intercostal spaces.

Through the open umbilicus of the type, on the flanks of the inside whorl, are seen a spiral of overdeveloped spines extending half way up the umbilical wall. These probably correspond to the fifth spiral of spines.

Striae on the vertical umbilical walls slope diagonally forward.

Only the type shows the nature of the spines, but there are molds which show the same general form and coarseness of rib as this specimen.

The largest specimen that might be included, about 90 mm. in diameter, is a septate, distorted internal mold inextricably imbedded in an extremely hard matrix. Septae are of the usual *Trachyceras* type, with a broad first lateral lobe and a pointed second lateral. Saddles appear rounded, unserrated, but this lack of serration may be due to weathering as a first lateral lobe also appears rounded, unserrated. The ribs are extremely coarse, especially near the umbilicus, where there are strong nodes. These would indicate about eight spirals of spines, as on the smaller (40 mm. D) type. In the same piece of rock matrix with this specimen are other, more finely ribbed forms of *Trachyceras;* also what appears to be *Clionites wheeleri*, n. sp. a pelecypod like *Sphaera whitneyi* Meek, and numerous baby ammonoids or pelecypods of microscopic size.

About half a dozen specimens of which only the internal molds are preserved might be assigned to this species on account of general form plus nature of ribs and nodes. One particular specimen, of which the dimensions are given, was described in my M.A. thesis as *Protrachyceras* on account of the rounded nodes next to the ventral furrow. The spines that rose from these nodes might, however, have been double pointed.

T. hylactor and T. böhmi (Mojsisovics, 1893, pl. 173, figs. 1, 3, 4) show similarity to the new species in the roughness of the

sculpture but have wider whorls at comparable diameters. Figure 4a especially could be compared to our type for size and ornamentation, but the umbilicus is wider. Cross section of our type looks more like figure 3b, which is a bigger specimen than 4b.

Some of the "Gruppe der *Trachycerata acanthica*" show a similarity to *T. bispinosum*, n. sp. *T. semiramis* Mojsisovics (1893, pl. 177, fig. 2) has similar arrangement of spines. It does not, however, have the two strong rows of double-pointed spines on the venter.

TRACHYCERAS (TRACHYCERAS) TRISPINOSUM Johnston, n. sp.

Plate 68, figures 1–3

	D	H/D	W/D	U/D	H/W	S[1]
(1)	33	0.52	0.55	0.21	0.95	11

[1] S = number of spirals of spines on a side.

(1) *T. trispinosum*, n.sp., pl. 68, figs. 1–3, type. The shell was larger than 33 mm. D, but measurements are only for the uncrushed parts.

Number of specimens, one (12?).

This species may be merely a more finely ornamented variety of *T. bispinosum*. It has one outstanding character, revealed only after very careful picking-away of the matrix, namely: a triple-pointed spine on either side of the ventral furrow. The point of this spine farthest from the furrow is the highest, the spine nearest the furrow the lowest. The spines in the next spiral towards the umbilicus are double-pointed. Then follow two smaller spirals, a larger spiral where ribs sometimes fork, three smaller spirals, and the larger umbilical spiral, which may be double-pointed and at which from one to three ribs originate. The nodes underlying the triple-pointed ventral spines give no indication of their three-pointed nature but would rather make one believe the specimen were a *Protrachyceras* with single-pointed spines next to the ventral furrow.

Perhaps a dozen specimens might be assigned to this species, but only one shows the true nature of the shell ornamentation. This specimen required about a week of cleaning under the binocular microscope using a darning needle in a pin-vise.

REFERENCES

ARTHABER, GUSTAV VON, *1911*, Die Trias von Albanien: *Beitr. Paläontologie Oesterr.-Ungarns u. des Orients*, Band 24, pp. 169–277, pls. 17–24, 10 text figs.

——, *1914*, Die Trias von Bithynien (Anatolien): *idem*, Band 27, pp. 85–206, pls. 11–18, 19 text figs.

——, *1927*, Ammonoidea Leiostraca aus der oberen Trias von Timor: *Jaarb. mijnwezen Ned.-Indië, Verhandellingen*, Jaargang 55 (1926), Gedeelte 2, pp. 1–174; Atlas (bound separately) pls. 1–20.

BERNDT, HORST, *1934*, Trias und Jura des Ostbalkans: *Sächs. Akad. Wiss., Math.-phys. Kl., Ber.*, Band 86, Heft 1, pp. 3–104, pls. 1–4, text figs. 1–3, 1 insert (geol. map: "Ostbalkanische Klippenzone auf Blatt Tekenlik. Massstab 1:80000").

BRONN, HEINR. G., *1832*, Die Versteinerungen des Salza-Thales in Beziehung auf Lill von Lilianbach's Beschreibung dortiger Gebirgs-Formationen: *Neues Jahrb.*, pp. 150–182.

CAMERON, EUGENE N., *1939*, Geology and mineralization of the northeastern Humboldt Range, Nevada: *Geol. Soc. America, Bull.*, vol. 50, pp. 563–634, 6 pls., 23 figs.

DIENER, CARL, *1900*, Die triadische Cephalopoden-Fauna der Schiechling-Höhe bei Hallstatt: *Beitr. Paläontologie Oesterr,-Ungarns u. des Orients*, Band 13, Heft 1, pp. 3–42, pls. 1–3.

——, *1906*, Fauna of the *Tropites*-limestone of Byans: *Palaeontologia Indica*, ser. 15 (Himalayan fossils), vol. 5, no. 1, pp. i–v, 1–201; pls. 1–17.

——, *1908a*, Upper-Triassic and Liassic faunae of the exotic blocks of Malla Johar in the Bhot Mahals of Kumaon: *idem*, vol. 1, part 1, pp. i–iii, 1–100, pls. 1–16.

——, *1908b*, Ladinic, Carnic and Noric faunae of Spiti: *idem*, vol. 5, no. 3, pp. 1–157, pls. 1–24.

——, *1909*, The fauna of the *Traumatocrinus* limestone of Painkhanda: *idem*, vol. 6, no. 2, pp. i–ii, 1–39, pls. 1–5.

——, *1915*, Cephalopoda triadica: *Fossilium catalogus*, I: *Animalia;* editus a F. Frech; Pars 8; W. Junk, Berlin; pp. 1–369.

——, *1917*, Ueber Ammoniten mit Adventivloben: *K. Akad. Wiss. Wien, Denkschr.*, Band 93, pp. 139–200, pls. 1–2.

——, *1919*, Neue Ammonoidea Leiostraca aus den Hallstätter Kalke des Salzkammergutes: *idem*, Band 97, pp. 341–389, pls. 1–4, text figs. 1–19.

DITTMAR, ALPHONS VON, *1868*, Zur Fauna der Hallstädter Kalke. Nova aus der Sammlung des Herrn Hofrathes Dr. Fischer in München: *Geognostisch-paläontologische Beiträge*, München (Munich), Band 1, Heft 2, pp. 319–398 ("Text"), pls. 12–20 ("Atlas").

EMMONS, S. F., *1877*, Desatoya Mountains: *U. S. Geol. Expl. 40th Par., Rept.*, vol. 2, pp. 644–649.

FREBOLD, HANS, 1929, Faunistisch-stratigraphische Untersuchungen über die Trias Spitz-

bergens und der Edge Insel: *Naturwiss. Ver. Hamburg Abh.*, Band 22, Heft 3–4, no. 4, pp. 293–312, pls. 36–37, text figs. 1–3.

FRECH, FRITZ, *1907*, Die Hallstätter Kalke bei Epidauros (Argolis) und ihre Cephalopoden: *Neues Jahrb., Festband*, pp. 1–32, pls. 1–6.

——, *1911*, Neue Cephalopoden aus den Buchensteiner, Wengener und Raibler Schichten der südlichen Bakony mit Studien über die Wohnkammerlänge der Ammoneen und über die Lebensweise der Nautileen: *Resultate wiss. Erforschungen des Balatonsees* (now "*Magyar földrajzi tarsasag*, Budapest"), Band 1, Teil 1, Anhang "Palaeontologie der Umgebung des Balatonsees" 3, no. 4, pp. 1–74, pls. 1–11, text figs. 1–20. Also in a "Separat Abdruck," 1903.

GABB, W. M., *1864*, Description of the Triassic fossils of California and the adjacent territories: *California Geol. Survey, Paleontology* 1, pp. 17–35, pls. 3–6.

——, *1869*, Descriptions of some secondary fossils from the Pacific States: *Am. Jour. Conchology*, vol. 5, pp. 5–18.

GUGENBERGER, ODOMAR, *1928*, Ueber einige unbekannte Cephalopoden aus der karnisch-norischen Mischfauna des Feuerkogels bei Aussee: *Akad. Wiss. Wien. Math.-naturwiss. Kl., Sitzungsber.*, Abt. 1, Band 137, Heft 3–4, pp. 113–122, 1 pl. (not numbered or lettered).

HANNA, G. DALLAS, *1924*, Rectifications of nomenclature: *California Acad. Sci., Proc.*, ser. 4, vol. 13, no. 10, p. 180.

HAUER, FRANZ RITTER VON, Die Cephalopoden des Salzkammergutes aus der Sammlung Sr. Durchl. des Fürsten von Metternich. *Ein Beitrag zur Paläontologie der Alpen*. 47 pp., 11 pls., Wien (Vienna).

——, *1860*, Nachträge zur Kenntnis der Cephalopoden-Fauna der Hallstätter Schichten: *K. Akad. Wiss. Wien, Math.-naturwiss. Kl. Sitzungsber.*, Band 41, no. 14, pp. 113–150, pls. 1–5.

——, *1887*, Die Cephalopoden des bosnischen Muschelkalkes von Han Bulog bei Sarajevo: *idem, Denkschr.*, Band 54, Abt. 1, pp. 1–50, pls. 1–8.

HAUG, EMILE, *1894*, Les ammonites du permien et du trias: *Soc. geol. France, Bull.*, sér. 3, t. 22, pp. 385–412, text figs. 1–13.

HYATT, ALPHEUS, *1877*, (see MEEK, F. B., *1877*).

——, and SMITH, J. P., *1905*, The triassic cephalopod genera of America: *U. S. Geol. Survey, Prof. Paper* 40, 394 pp., 85 pls., 1 text fig. (table showing the relation of Triassic to Paleozoic genera of cephalopods).

KING, CLARENCE, *1876*, Geological and topographical atlas accompanying the report of the geological exploration of the Fortieth Parallel: Washington, D. C. (Map V "Nevada Basin" shows New Pass and the Desatoya Range).

——, *1878*, *U. S. Geol. Expl. 40th Par., Rept.*, vol. 1, pp. 268–278 (on the Star Peak group, "West Humboldt Range"), pp. 282–284, 630–632 (Desatoya Mountains).

KITTL, E. VON, *1908*, Beiträge zur Kenntnis der Triasbildungen der nordöstlichen Dobrudscha: *K. Akad. Wiss. Wien, Math.-naturwiss. Kl.*, Band 81, pp. 447–532, pls. 1–3, text figs. 1–17, 1 insert (geologic map).

KUTASSY, A., *1932*, Cephalopoda triadica II: *Fossilium Catalogus* I: *Animalia*. pars 56, W. Junk, Berlin, pp. III–IV, 371–382.

LAUBE, GUSTAV C., *1869a*, Ueber *Ammonites aon* Münster und dessen Verwandte: *K. Akad. Wiss. Wien., Math.-Naturwiss. Kl., Sitzungsber.*, Band 59, Abt. 1, Heft 1, pp. 7–16.

——, *1869b*, Cephalopoden.—Schluss. V. Abteilung. Die Fauna der Schichten von St. Cassian: *idem, Denkschr.*, pp. 49–106, 8 pls.

LEIDY, JOSEPH, *1868*, Notice of some reptilian remains from Nevada: *Acad. Nat. Sci. Philadelphia, Proc.*, pp. 177–178.

LINCOLN, F. C., *1923*, *Mining districts and mineral resources of Nevada*. Reno, Nevada Newsletter Publishing Co., pp. i–iv, 1–295; 1 insert (map of the State of Nevada showing counties and mining districts).

MARTELLI, ALESSANDRO, *1904*, Cefalopodi triasici di Boljevici presso Vir nel Montenegro: *Palaeontographia Italica*, vol. 10, pp. 75–140, pls. 5–14, text figs. 1–10.

MCLEARN, F. H., *1937*, New species from the Triassic Schooler Creek formation: *Canadian Field Naturalist*, vol. 51, no. 7, pp. 95–98, pl. 1.

MEEK, F. B., *1877*, Paleontology: *U. S. Geol. Expl. 40th Par. Report*, vol. 4, part 1, pp. 1–198, pls. 1–17.

MERRIAM, J. C., *1902*, Triassic Ichthyopterygia from California and Nevada: *California Univ., Dept. Geol. Sci., Bull.*, vol. 3, no. 4, pp. 63–108, pls. 5–16, text figs. 1–2.

——, *1908*, Triassic Ichthyosauria, with special reference to the American forms: *California Univ., Memoir* No. 1, 196 pp., 18 pls., 154 text figs.

——, *1938*, Published papers and addresses of John Campbell Merriam: *Carnegie Inst. Washington, Pub.* 500, 4 vols., 2672 pp., many pls. and text figs., numbered as in the original publications.

MOJSISOVICS, EDMUND VON, *1869*, Beiträge zur Kenntnisse der Cephalopoden-Fauna des alpinen Muschelkalkes: *K. k. geol. Reichsanstalt Wien., Jahrb.*, Band 19, Heft 4, (No.) 4, pp. 567–594, pls. 15–19.

——, *1870*, Beiträge zur Kenntnis der Cephalopoden-Fauna der önischen Gruppe: *idem, Jahrb.*, Band 20, Heft 1, (No.) 4, pp. 93–112, pls. 4–5.

——, *1873*, Die Mollusken-Faunen der Zlambach und Hallstätter Schichten: *idem, Abh.*, Band 6, Theil 1, Heft 1, 82 pp., 32 pls. (Covers *Orthoceras, Nautilus, Lytoceras, Phylloceras, Pinacoceras, Sageceras*, and in part *Arcestes*).

——, *1875*, Die Mollusken-Fauna der Zlambach- und Hallstätter-Schichten: *idem, Abh.*, Band 6, Theil 1, Heft 2, pp. 83–174, pls. 33–70. (Concludes *Arcestes*. Covers *Didymites* and *Lobites*).

——, *1879*, Vorläufige kurze Uebersicht der Ammoniten-Gattungen der mediterranen und juvavischen Trias: *idem, Verh.*, pp. 133–143, 1 table.

——, *1882*, Die Cephalopoden der mediterranen

Triasprovinz: *idem, Abh.*, Band 10, pp. I–X, 1–322; pls. 1–94.

——, *1893*, Die Cephalopoden der Hallstätter Kalke: *idem, Abh.*, Band 6, Hälfte 2, 835 pp. ("Text"); pls. 71–200 ("Atlas").

——, *1896*, Beiträge zur Kenntnis der obertriadischen Cephalopoden-Faunen des Himalaya: *K. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr.*, Band 63, pp. 575–701, pls. 1–22, 8 text figures (unnumbered).

——, *1899*, Upper Triassic cephalopod faunae of the Himalaya: *Palaeontologia Indica*, ser. 15 (Himalayan Fossils), vol. 3, part 1, 158 pp., 22 pls. (Translation by Dr. Arthur H. Foord and Mrs. A. H. Foord into English of Mojsisovics' article, 1896, cited above.)

——, *1902*, Die Cephalopoden der Hallstätter Kalke: *K. k. geol. Reichsanstalt Wien, Abh.*, Band 6, Abt. 1, Sup. Heft, pp. 175–356, pls. 1–23.

MULLER, S. W., *1936*, Triassic coral reefs in Nevada: *Am. Jour. Sci.*, ser. 5, vol. 31, no. 183, pp. 202–208.

——, and FERGUSON, H. G., *1939*, Mesozoic stratigraphy of the Hawthorn and Tonopah quadrangles, Nevada: *Geol. Soc. America, Bull.*, vol. 50, pp. 1573–1624, 5 pls., 4 text figs., 4 tables (including 1 inserted "Correlation table").

MÜNSTER, G., *1834*, Ueber das Kalkmergel-Lager von *St. Cassian in Tyrol* und die darin vorkommenden Ceratiten: *Neues Jahrb.*, pp. 1–15, pls. 1–2.

——, und WISSMANN, DR., *1841*, Beiträge zur Geognosie und Petrefaktenkunde des südöstlichen Tirols vorzüglich der Schichten von St. Cassian: *Beiträge zur Petrefacten-Kunde . . . herausgegeben von G. Graf zu Münster*, Heft 4, Beyreuth.

POMPECKJ, J. F., *1894*, Ueber Ammonoideen mit "anormaler Wohnkammer": *Ver. vaterl. Naturkunde Württemberg, Jahresh.*, pp. 220–290, pl. 4, text figs. 1–4.

RAYMOND, R. W., *1869*, Mineral resources of the States and territories west of the Rocky Mountains: *House of Representatives, 40th Congress, 3rd session, Ex. Doc.* 54, 256 pp., numerous text figs. (not numbered).

REIS, OTTO M., *1901*, Eine Fauna des Wettersteinkalkes. I. Theil. Cephalopoden: *Geognostische Jahreshefte, Jahrg.* 13, München (Munich), pp. 71–105, pls. 2–7.

RENZ, KARL, *1906*, Trias und Jura in der Argolis: *Deutsche geol. Gesell., Zeitschr.*, Band 58, pp. 379–388.

——, *1911*, Die mesozoischen Faunen Griechenlands. I. Die triadischen Faunen der Argolis: *Palaeontographica*, Band 58, Lief. 1, 2, pp. 1–104, pls. 1–7, text figs. 1–15.

——, *1922*, Neue griechische Trias Ammoniten: *Naturf. Gesell. Basel, Verh.*, Band 33, pp. 218–255, pls. 6–8, text fig. 1.

SALTER, J. W., and BLANFORD, H. F., 1865, *Paleontology of Niti in the Northern Himalayas.* Calcutta, 112 pp., 23 pls., text figs.

SCHNETZER, ROBERT, *1934*, Die Muschelkalkfauna des Oefenbachgrabens bei Saalfelden: *Palaeontographica*, Band 81, Abt. A, Lief. 1–3, pp. 1–160, pls. 1–6, text figs. 1–15, 1 insert (table of geologic and geographic occurrence of species).

SIMIONESCU, IOAN, *1913*, Fauna amonitilor triasici dela Hagighiol. Les ammonites triassique de Hagighiol (Dobrogea): *Acad. Română; publicaţiunile fondului Vasile Adamachi*, vol. 5, no. 34; Studii geologice şi paleontologice din Dobrogea, 6; Bucuresti (Bucharest), pp. 271–370, pls. 1–9, 78 text figs. (Résumé in French.)

SMITH, J. P., *1904*, The comparative stratigraphy of the marine Trias of western America: *California Acad. Sci., Proc.*, ser. 3 (Geology), vol. 1, no. 10, pp. 323–430, pls. 40–49, 1 correlation table (between pp. 334–335).

——, *1914*, The Middle Triassic marine invertebrate faunas of North America: *U. S. Geol. Survey, Prof. Paper* 83, 254 pp., 99 pls., 1 insert (interregional correlation table of the Trias).

——, *1927*, Upper Triassic marine invertebrate faunas of North America; *idem, Prof. Paper* 141, pp. I–IV, 1–262; pls. 1–121.

SPATH, L. F., *1934*, The Ammonoidea of the Trias: *Catalogue of the Fossil Cephalopoda in the British Museum* (*Natural History*), Part IV, London, British Museum, pp. i–xvi, 1–521; pls. 1–18, text figs. 1–160, tables 1–4.

STOLICZKA, FERDINAND, *1865*, Geological sections across the Himalaya Mountains from Wangtu bridge on the river Sutlej to Sungdo on the Indus; with an account of the formations in Spiti accompanied by a revision of all known fossils from that district: *India Geol. Survey Mem.*, vol. 5, part 1, art. 1, pp. 1–154, pls. 1–9.

SUESS, E., *1865*, Über die Cephalopoden-Sippe *Acantholeuthis: K. Akad. Wiss. Wien, Math.-naturwiss. Kl., Sitzungsber.*, Band 51, Abt. 1, Heft 1–5, pp. 225–244, pls. 1–4.

TOMLIN, J. R. LE B., *1931*, Some preoccupied generic names: *Malacol. Soc. London, Proc.*, vol. 19, pp. 174–175.

TOMMASI, ANNIBALE, *1899*, La fauna dei calcari rossi e grigi del Monte Clapsavon nella Carnia occidentale: *Palaeontographia Italica*, vol. 5, pp. 1–54, pls. 1–7, text figs. 1–8.

TORNQUIST, A., *1898*, Neue Beiträge zur Geologie und Palaeontologie der Umgebung von Recoaro und Schio (im Vicentin). I (Beitrag) Die nodosen Ceratiten: *Deutsche geol. Gesell., Zeitschr.*, Band 50, Heft 2, pp. 209–233, pls. 8–10.

——, *1899*, Neue Beiträge zur Geologie und Palaeontologie der Umgebung von Recoaro und Schio (im Vicentin). II. (Beitrag). Die *Subnodosus*-Schichten: *idem*, Band 50, Heft 4, pp. 637–694, pls. 20–23.

TOULA, F., *1896*, Eine Muschelkalkfauna am Golfe von Ismid in Kleinasien: *Beitr. Paläontologie Oesterr.-Ungarns u. des Orients*, Band 10, pp. 154–191, pls. 18–22, text figs. 1–8.

U. S. DEPT. INTERIOR, *1930*, General Land Office map of the State of Nevada; scale: 1 inch = 12 miles.

WELTER, OTTO A., *1915*, Die Ammoniten und Nautiliden der ladinischen und anisischen Trias

von Timor: *Paläontologie von Timor*, Lief. 5, Heft 10, pp. 71–136, pls. 83–95, text figs. 1–29.

WHEELER, HARRY E., *1939, Helicoprion* in the Anthracolithic (late Paleozoic) of Nevada and California, and its stratigraphic significance: *Jour. Paleontology*, vol. 13, no. 1, pp. 103–114, text figs. 1–4, 1 table.

WHITE, A. F., *1869, Report of the State Mineralogist of Nevada for the years 1867 and 1868*, pp. 1–96.

WULFEN, F. X. VON, *1793, X. Wulfens Abhandlung von kärnthenschen pfauenschweifigen Helmintholith, oder dem sogenannten opalisierenden Muschelmarmor:* Erste Ausgabe, etc., Erlangen, 124 pp., 33 pls. (colored).

——, *1790, idem*, another edition, Nurnberg.

YABE, HISAKATSU, and SHIMIZU, SABURÔ, *1927*, The triassic fauna of Rifu, near Sendai: *Tohoku Imp. Univ., Sci. Repts.*, ser. 2, vol. 11, no. 2, pp. 101–136, pls. 10–14, text figs. 1–8.

A DISSERTATION SUBMITTED TO THE FACULTY OF THE CATHOLIC UNIVERSITY OF AMERICA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY. MANUSCRIPT RECEIVED BY THE EDITOR FEBRUARY 11, 1941.

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SILICIFIED TRENTON TRILOBITES

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ABSTRACT—The material studied includes five species of Trilobita belonging to five different genera. The undistorted silicified specimens, freed from the matrix by etching with acid, give exceptional opportunity for study of the ventral as well as the dorsal surface of the test.

For the first time the complete developmental stages of a calymenid, *Flexicalymene senaria*, are described. The protaspid hypostoma is relatively large, and the lateral and posterior borders bear eight spines. The protaspid and meraspid test is spiny, the spines being reduced to tubercles in the adult. The cephalon is proparian; the glabella, at first widest anteriorly, becomes bell-shaped in outline. The development of an odontopleurid has not previously been described, but the new genus *Diacanthaspis* is known in both the meraspid and holaspid degrees. The young test bears many long spines, the adult more numerous shorter spines. The arrangement of new spines appearing on the developing cranidium is symmetrical and apparently dependent upon the original segments that fused to form the cephalon. During development the posterior part of the glabella and fixed cheeks and the occipital ring appear to increase greatly, both in length and convexity, relative to, and therefore at the expense of, the rest of the cephalon. At meraspid degree 0 the narrow rolled fringe of *Cryptolithus tesselatus* has one row of pits. At about degree 3 the fringe is very similar to that of the adult. During development the outline of the pygidium changes from subsemicircular to subtriangular. To ensure complete closure in enrollment throughout life the outline of the inner edge of the lower lamella of the fringe changes with that of the pygidium. The transitory pygidia of *Ceraurus pleurexanthemus* show the development of the appendifers and the articular facet between the segments. Thus additional light is thrown on the problem of the origin and growth of the postcephalic segments. The beautifully preserved ventral surface of the holaspid test of *Ceraurus* and *Flexicalymene* has given new information on the doublure and anterior pits of the cephalon, the hypostoma, the appendifers, and the thoracic articulation. In these two genera the hypostoma appears to be attached by the hypostomal suture and a pair of articulating joints between the anterior wings of the hypostoma and the anterior pits of the cephalon.

In the third part of the paper the new information is discussed in relation to present views on the eye and the segmentation of the cephalon, the attachment of the hypostoma, the appendifers, the development, and the enrollment of the trilobite.

I. INTRODUCTION

THE trilobites described and discussed in the following pages come from two localities in Virginia. Almost all are from loose blocks of limestone on a hillside about 2½ miles north-northeast of Spring Hill, Augusta County. A lesser amount of similar material comes from a point about 3 miles north-northeast of Long Glade.

The fauna of which these trilobites are a part is of Trenton age, possibly the same as that of the Denmark member of the Sherman Fall formation (Kay, 1937, pp. 250, 268).

Certain blocks of the limestone, when etched in a five per cent solution of hydrochloric acid, have yielded an abundant variety of well-silicified trilobites of all sizes. These specimens are thus completely freed from the matrix, and there seems to be no reason to believe that they are not entirely undistorted. Each element of the test—the cranidium, free cheeks, hypostoma, thoracic segments and pygidium—is generally separate from the others, though a few complete enrolled specimens of the cryptolithid are known. Therefore the developmental stages cannot be divided into the meraspid and holaspid degrees; in the description the development of the cephalon, thorax, and pygidium have been treated separately, and the largest specimens taken to be the holaspid trilobite. The silicification appears to have taken place by the formation of an extremely thin layer of silica on each side of the original test, which has then been removed. The two layers may be well seen, for example, in the photographs of *Flexicalym-*

ene (pl. 72, figs. 44, 47). The finest detail has been preserved in this manner. The specimens are very delicate and have to be handled with considerable care. A few were broken while being photographed, and were thus incomplete when photographed in reverse view. Particles of silica that cannot be removed without damage to the specimen adhere to the surface and may be seen in some of the pictures.

Almost all the material was collected and prepared by Dr. G. Arthur Cooper, of the U. S. National Museum, at whose invitation I undertook this study. I am very grateful indeed to Dr. Cooper for the privilege of working on these beautifully preserved trilobites. I have also had the privilege and pleasure of discussing the organization of trilobites with Dr. Percy E. Raymond, and he has helped me greatly by his encouragement and criticism. Dr. Raymond allowed me access to his collections of American and European odontopleurids, including the types of *Onchaspis confraga* and *Diacanthaspis? parvula*. Through the kindness of Dr. H. E. Vokes, of the American Museum of Natural History, I received the type of *Leonaspis? trentonensis* on loan, and Dr. Winifred Goldring, of the New York State Museum, sent me further material of this species. Dr. Carl O. Dunbar has kindly read my manuscript and offered many valuable suggestions.

In the systematic descriptions the terminology of Warburg (1925, pp. 1–7) has been followed with few exceptions. I have preferred to number the glabellar lobes from the posterior pair forwards, both in order to follow Shirley (1936) and Öpik (1937), and for convenience in discussing the segmentation of the cephalon. The terms epistoma and epistomal suture have been used in preference to rostrum and rostral suture. In describing the trinucleid I have employed the same terminology as previously (1940, 1941), and used new terms only in describing the arrangement of the spines on the cephalon of the odontopleurid.

No attempt has been made to give complete synonymies of *Flexicalymene senaria*, *Ceraurus pleurexanthemus*, or *Cryptolithus tesselatus*. The most recent writings on the latter two species have references to previous work, and Bassler (1915, p. 201, pp. 295–296) has many more. Bassler (1915, p. 169) gives also many references to writings on *Flexicalymene senaria*.

As the figures forming the plates were made of the smallest size that would show the desired amount of detail, the magnification at which each photograph was taken varies according to the size of the specimen, and the pictures of a developmental series of cranidia, for example, do not show at a glance the actual differences in size.

II. SYSTEMATIC DESCRIPTIONS

Family CALYMENIDAE Milne Edwards, 1840

Genus FLEXICALYMENE Shirley, 1936

FLEXICALYMENE SENARIA (Conrad), 1841

Plate 72, figures 1–27, 31–34, 38–40, 42–47, text figure 1.

Calymene senaria CONRAD, *1841*, New York Geol. Survey, Ann. Rept. 5, pp. 38, 49.

Cephalon subsemicircular in outline, about twice as wide as long, very strongly convex.

Glabella subtriangular in outline, with rounded anterior end; convex and standing high above the cheek lobes and reaching a little farther forwards. Three pairs of lateral glabellar lobes, graduated in size. First

1

FIG. 1—Hypostoma of the protaspis of *Flexicalymene senaria*. Drawn from the original of plate 72, figure 2.

lobes large, quadrilateral in outline, defined by the first glabellar furrows, which are straight, deep, directed obliquely backward, and bifurcate, the posterior branches being connected by shallow lobe grooves with the occipital furrow. Second lobes smaller, subrectangular in outline, the second glabellar furrows straight, directed obliquely backward, and connected by shallow lobe grooves with the anterior branch of the first glabellar furrows. Third lobes distinct, defined anteriorly by the very short, straight glabellar

furrows, which are shallower and commence on the glabella just within the axial furrows. Occipital furrow deep behind the first lobes, shallowing and swinging forward in a gentle curve axially. Occipital ring longest axially, posterior margin curving forward to the axial furrows, doublure about half its length, conspicuously striated.

Axial furrows moderately deep, broad anteriorly, with shallow circular anterior pits, posteriorly narrowing and curving inwards behind the first lobes. On the inner surface the anterior pits appear as low rounded bosses, the anterior slope of which is excavated into a shallow pit.

Preglabellar field strongly recurved, without any subsidiary ridge, the narrow margin turned down and bounded by the epistomal suture.

Fixed cheeks strongly convex, their shape determined by the position of the eyes opposite the second glabellar lobes. An inconspicuous eye ridge runs obliquely from the palpebral lobe to a point opposite the third glabellar lobes. Posterior marginal furrows moderately deep, shallowing laterally. Posterior border short and without doublure adjacent to the axial furrows, lengthening and with doublure laterally. On the margin of the extremities a low rounded tubercle, the remnant of the genal spine.

Free cheeks subtriangular in outline, descending in a steep convex slope to the thick, rolled margin. In ventral aspect the doublure is strongly flexed upwards, broadest anteriorly, and projecting under the lateral extremities of the preglabellar field, and bounded by the connective sutures.

Epistoma unknown.

Hypostoma subrectangular in outline. Middle body moderately convex, divided by a very shallow furrow into the anterior and posterior lobes. Anterior border strongly flexed ventrally at about halfway between the anterior furrow and the margin. The anterior wings are extended laterodorsally, with a deep pit on the ventral side near the anterolateral edge. On the inner (dorsal) surface this pit appears as a stout rounded boss. Lateral and posterior furrows continuous, U-shaped, with distinct deepenings at the anterior and posterior ends of the lateral furrows. The middle furrow runs into the anterior pair of deepenings. Lateral borders narrow, flexed ventrally. Posterior border flat, forked, the notch reaching forward almost to the posterior furrow. Lateral and posterior borders with doublure, which extends inwards as far as the lateral and posterior furrows and is crossed at the small posterior wings by a conspicuous fold. The hypostoma shows noticeable variability in the convexity of the middle body and the outline of the forked posterior border.

The ornamentation of the cranidium consists of tubercles of varying size, closely placed on the glabella, occipital ring, and the margin of the preglabellar field. On the latter the tubercles become more scattered away from the margin and are absent in the bottom of the preglabellar furrow. The deepest parts of the glabellar, occipital, axial and posterior marginal furrows are also without ornament. Anterior to the eye the ornamentation of the fixed cheeks is similar to that of the glabella, but posterior to the eye the ornament is much less prominent, the tubercles being smaller and more widely spaced. The free cheeks are ornamented similarly to the glabella, the tubercles being closely packed on the marginal roll. The doublure is smooth.

Shirley (1936, p. 414) has described the ornamentation of a calymenid in which the tubercles are

> pierced by a hole which is situated, not at the highest point, but a little way down that side which would be away from the current when the trilobite moved forward. These apertures are connected with canals which traverse the test perpendicular to the surface.

Some of the cephala of the material here described show such openings in tubercles, situated on the glabella, the preglabellar field, the occipital ring, and possibly the margins of the free cheeks (see pl. 72, figs. 40, 45). Casts of canals traversing the test are also visible in the glabella and preglabellar field of some specimens. The ventral surface of the cranidium is apparently smooth, except for the prominent canal openings in the median area of the glabella and preglabellar field (see pl. 72, figs. 44, 47).

One specimen of the hypostoma is weakly ornamented on the ventral surface with fairly closely placed tubercles, most prominent near the anterior margin.

Thorax of 13 segments (observation on

whole specimens from Trenton Falls). Axial ring strongly convex, articulating furrow deep, articulating half ring elevated. The pleurae widen laterally, extremities rounded and without spines. The fulcrum in anterior segments is farther from the axial furrows than in posterior segments, and the posterior pleurae are more strongly flexed ventrally, so that the thorax is narrow and more strongly convex posteriorly than anteriorly. Pleural furrows deep in the inner parts, shallowing and disappearing in the lateral parts. At the axial furrows an articulating socket on the anterior margin, a process on the posterior margin. At the fulcrum an articulating process on the anterior margin, a socket on the posterior margin. Corresponding processes and sockets on the margin of the cephalon and pygidium. Posterior axial doublure striated. The lateral parts of the pleurae with a doublure on the posterior margin and around the extremities, on the anterior edge the doublure extends inwards only a short way and is thickened to form a process. In enrollment the lateral parts of the pleurae slide underneath those of the next anterior segment, and these pleural processes limit the movement. Pleurae without facets. Axial ring and pleurae ornamented with closely spaced medium-sized tubercles.

Pygidium subtriangular in outline, very strongly convex. Rachis with five distinct and one less distinct segments, posteriorly with rounded termination a short distance within the margin. First segment with articulating furrow and half ring. Axial furrows shallow. Five distinct and one less distinct pleural segments. Posteriorly to the rachis without segmentation. First pleurae with strong pleural furrow axially, shallowing laterally, prominent facet at the anterior extremities. The next three pleurae with shallow pleural furrows laterally. Margin smoothly curled under, doublure flexed strongly inwards. At the anterior extremities of the first pleurae the doublure is thickened to form a process corresponding to that on the thoracic pleurae, and performing the same function as the facets move under the last thoracic segment in enrollment. The pygidium is ornamented with medium-sized, closely-spaced tubercles, except on the facets and the doublure.

Discussion: The name *Calymene senaria* was proposed by Conrad (1841, pp. 38, 49) for the Trenton species of calymenid, and I have therefore regarded the present material as belonging to this species, and placed it in the genus *Flexicalymene* Shirley (1936, p. 395).

Development.—THE PROTASPID: The outline is subcircular, the whole shield strongly convex, sloping steeply laterally and posteriorly, a little less steeply anteriorly. The rachis is widest anteriorly; at about half the length is about one-quarter that of the whole shield, and posteriorly the termination just within the margin is rounded. A long anterior segment, and four further, shorter axial segments are visible, the posterior possibly representing the occipital segment. The subtriangular posterior part would thus represent the rachis of the pygidium. The axial furrows are broad and shallow.

The anterior edge of the short preglabellar field is straight and bears some ten short spines, the lateral pair being stouter and longer.

The eyes lie just within the anterior margin and immediately lateral to the large spines on the margin of the preglabellar field. The palpebral lobes are connected by a broad low ridge, flanked by wide shallow furrows, to the anterior end of the axial furrows, which are rather wide, probably representing the position of the anterior pits. The facial sutures are extremely short, and the free cheeks, which must have been extremely narrow, unknown. A pair of very stout spines are situated on the margin immediately posterior to the point where it is cut by the posterior branch of the facial suture. Posteriorly to the eyes the pleural regions of the shield are smooth, without indication of segmentation.

Posterolaterally and posteriorly the margin has four distinct pairs of spines. The first pair are situated opposite the furrow in the rachis, which is presumed to separate the cephalon and pygidium, and are directed posterolaterally. The second pair are directed almost directly backwards, the third point backwards and inwards, and the fourth more strongly so.

In ventral aspect the posterior margin of the protaspis, with the four pairs of spines, is seen to be rolled under in a narrow doublure. It might be inferred from this latter

fact that this posterior spined region is one unit, and represents the pygidium, and I therefore do not think that the first pair of spines represent the genal spines. It may be also that the two most prominent pairs of spines adjacent to the facial sutures are the procranidial and metacranidial spines of Raw (1925, p. 232).

Attached to the ventral side of one specimen of the protaspis is what appears to be the hypostoma. It is not lying in natural position, but has been displaced sideways and rotated somewhat (pl. 72, fig. 2; text fig. 1). The middle body of the hypostoma is pear-shaped, the posterior end bluntly pointed, strongly convex, and well defined by the furrows laterally and posteriorly. The anterior border is narrow, flexed gently ventrally, and with gently curved anterior margin. Anterior wings flexed strongly dorsally. Lateral borders narrow anteriorly, widening rapidly posteriorly and continuous with the broad posterior border, across which the hypostoma attains its greatest width. The posterior border is slightly notched but is most remarkable in bearing four pairs of short, thick spines. The first pair is situated opposite a point at about two-thirds the length of the middle body and is directed outwards and slightly backwards. The succeeding pairs are placed at equal intervals and directed more nearly backwards, the last two pairs pointing inwards and backwards.

THE CEPHALON: The smallest isolated cranidium (0.7 mm. in length) is subsemicircular in outline, strongly convex. The glabella is long and narrow, widest anteriorly, strongly convex. It is almost crossed by the shallow furrows, the three posterior segments of approximately equal length and shorter than the anterior lobe. Occipital furrow straight, deeper than the glabellar furrows. Occipital ring with the posterior margin gently curved, large, low median tubercle, and narrow doublure. Preglabellar field narrow, flat, the margin very gently curved, and bearing a number of short spines directed forwards. Axial furrows straight, shallow.

Fixed cheeks with eyes situated far forwards and close to the margin; smooth, strongly convex, and sloping almost vertically down laterally; prolonged posteriorly into a stout, backwardly directed genal spine, which itself bears short, small spines. Posterior marginal furrow indistinct. Posterior margin with doublure laterally.

Free cheeks unknown.

The next largest cranidia have the glabella widest posteriorly, relatively long and narrow, and the first and second glabellar lobes may be distinguished; the third lobes very faint, the glabellar furrows short and shallow, especially the third pair. The occipital furrow is deeper and curved slightly anteriorly. The occipital ring bears a short, stout median spine and several small spines on the posterior margin. Axial furrows with shallow anterior pits. The preglabellar field is a little wider, the anterior margin more curved, and bearing numerous short spines.

The eyes are farther back, opposite a point about one-third the length of the glabella, and proportionately large. The anterior branches of the facial sutures converge, the posterior cut the anterior edge of the genal spine on the ventral side. The highest point of the fixed cheeks is at the eye, and they slope steeply down to the axial furrows and laterally. The stout genal spine is directed slightly outwards, and bears small spines on itself.

Free cheeks unknown.

The axial region of the glabella and the fixed cheeks, especially near the palpebral lobes and genal angles, are ornamented with short spines and tubercles. In the axial region of the glabella one specimen shows paired spines, rather stouter than the others, the first, second and third pairs opposite the first, second and third glabellar lobes, the fourth situated about midway on the anterior lobe.

Slightly larger cranidia have the glabella about as long as wide. The three pairs of glabellar lobes are small, distinct, the glabellar furrows wide and shallow. The occipital ring with the median spine rather shorter. The preglabellar field is flexed gently upwards, rather wider, the anterior margin more curved, still with numerous short spines. Axial furrows shallow, shallow anterior pits.

Palpebral lobes large. Facial sutures converging slightly forwards. Posterior branch running to the genal angle and across the doublure immediately anterior to the spine.

The ornamentation consists of numerous short spines and tubercles, fairly closely spaced over the cephalon, except in the furrows. The spines are reduced in length as compared to smaller cephala. The paired spines on the glabella are considerably reduced.

With increasing size the cephalon approaches the proportions of the adult. The glabella increases in width, especially posteriorly, becomes more rounded anteriorly and more convex, standing higher above the cheek lobes. The glabellar, occipital and axial furrows become deeper and narrower, and the glabellar lobes consequently more distinct. The preglabellar field becomes wider, and the anterior margin more curved, and is more strongly flexed dorsally.

The palpebral lobes become proportionately less large.

The spines, including the genal spines, are gradually reduced in length, those on the margin of the preglabellar field remaining conspicuous to a rather late stage.

A cephalon of length 2.9 mm. (pl. 72, fig. 14), differs from the adult cephalon in that the glabella is markedly narrower, the preglabellar field appearing slightly shorter, and bearing numerous short spines. The occipital spine is represented by a large tubercle, and there are short, stout, genal spines. The ornament is more coarsely tuberculate. With increasing size these differences gradually disappear.

THE HYPOSTOMA: The smallest hypostoma in the material, apart from that of the protaspis described above, is shorter than the adult and has the posterolateral borders much reduced as compared to the protaspid. It is forked, and each of the "blades" bears a short spine. The middle body is oval in outline and divided by the shallow middle furrow. A pair of wide, shallow pits lie at the anterior ends of the lateral furrows. With increasing size the adult outline is attained, and the spines on the "blades" are reduced and disappear.

THE THORAX: The smallest axial segments in the material exhibit all the features of the adult, and in addition bear on the axial ring and the posterior pleural bands short spines similar to those on the small cephala.

THE PYGIDIUM: The smallest pygidia are less convex than the adult, with six distinct segments. The axial rings and pleurae are ornamented with numerous short spines, the pleurae without pleural furrows. On the dorsal extremities of the pleurae two divergent spines arise from a common base, and a very short, broad spine, directed outwards and backwards, arises on the margin. At this stage the margin is only slightly curled under. At a little larger size it is more curled, and an additional spine appears between the double and single marginal spines. The next larger size shows the margin rolled under, forming the doublure, and without the spines. With increasing size the pygidium becomes more convex as the pleurae are more sharply bent down. The spines on the axial rings and pleurae are gradually reduced, and the pleural furrows developed.

Discussion.—Early stages in the development of *Flexicalymene senaria* have been described by Ruedemann (1912, p. 120, pl. 9, figs. 7–9), and Raymond (1917, p. 210) has stated that it is then proparian. The present material is well preserved and adds much that is new to the knowledge of the development of the species, and confirms Raymond's statement.

One of the most striking features of the early stages is the spinyness, a fact not shown by Ruedemann's specimens. The whole dorsal surface of the test and the posterolateral margins of the hypostoma are spiny. These spines are gradually reduced, the most persistent being the genal spines, and some at least seem to be represented in the adult by tubercles. In this connection, if Shirley is right in suggesting that some of these tubercles are the seat of tactile hairs, and my observations on the structure of the tubercles of the adult confirm his, then some of the spines may possibly have possessed a tactile function, as well as perhaps being an adaptation to the planktonic mode of life (cf. Swinnerton, 1915, p. 544).

Great changes occur in the glabella during development. It is at first long and narrow, widest anteriorly, with four annulations, the anterior markedly longest. In this it corresponds in general with Ruedemann's figure (7, pl. 9), but the second annulation is not wider than the others. At a very early stage the furrows cease to cross the glabella

and outline the glabella lobes. At this stage the paired spines are notable, but their arrangement is soon obscured by additional spines and tubercles. With increasing size the glabella becomes wider, more convex, and widest posteriorly, and the furrows become deeper. The occipital ring is notable for the median spine, which is reduced to a tubercle and not discernible in the adult. The preglabellar field is at first short, flat, and with a straight anterior margin, it gradually becomes longer and more strongly flexed dorsally, and the anterior margin becomes curved. The numerous prominent spines on the margin are represented by tubercles in the adult.

At the earliest stage at which the dorsal shield is known the eyes are present on the anterior margin of the fixed cheeks and migrate to the adult position quite early in the development. The small free cheeks are not known.

The spiny margin of the pygidium in the earliest stages is in accord with the spiny nature of the rest of the test.

Dimensions.—The sagittal lengths and maximum widths of *Flexicalymene senaria* are enumerated below. The length and width of the cephalon and glabella of 13 individuals are, respectively, 0.7, ?, 0.5, 0.2 mm. (pl. 72, fig. 3); 1.3, 1.2, 0.8, 0.6 mm. (pl. 72, fig. 4); 1.3, ?, 0.9, 0.8 mm. (pl. 72, fig. 5); 1.8, ?, 1.1, 1.0 mm. (pl. 72, fig. 6); 1.8, ?, 1.2, 1.1 mm. (pl. 72, fig. 7); 2.1, ?, 1.4, 1.3 mm. (pl. 72, fig. 8); 2.8, 4.5, 1.7, 1.6 mm.; 2.9, ?, 1.9, 1.8 mm. (pl. 72, fig. 14); 3.8, 5.8, 2.2, 2.5 mm. (pl. 72, fig. 15); 4.2, 6.6, 2.5, 3.0 mm.; 4.8, 7.4, 2.7, 3.1 mm.; 5.5, 8.6, 3.2, 3.9 mm.; 7.9, 12.2, 4.2, 5.4 mm. (pl. 72, fig. 16).

The length and width of five protaspes are, respectively, 0.7, 0.6 mm. (pl. 72, fig. 2); 0.7, ? mm.; 0.8, 0.8 mm.; 0.6, 0.6 mm; 0.6, 0.6 mm.

The length and width of seven hypostomae are, respectively, 0.4, 0.4 mm. (pl. 72, fig. 2); 1.1, 0.9 mm. (pl. 72, fig. 34); 1.5, 1.2 mm.; 2.5, 1.9 mm. (pl. 72, fig. 43); 4.5, 3.8 mm. (pl. 72, fig. 46); 4.8, 4.2 mm.; 4.2, 3.3 mm.

The length and width of seven pygidia are, respectively, 1.5, 1.8 mm. (pl. 72, fig. 20); 2.0, 2.5 mm.; 3.0, 3.8 mm.; 3.0, 4.0 mm.; 3.8, 4.7 mm.; 4.2, 5.4 mm.; 7.0, 8.3 mm.

Family CHEIRURIDAE Hawle and Corda, 1847

Genus CERAURUS Green, 1832

CERAURUS PLEUREXANTHEMUS Green, 1832
Plate 73, figures 1–40

This species has been redescribed by Raymond and Barton (1913, pp. 528–533, pl. 1, fig. 1; pl. 2, figs. 1, 2, 7), and my material agrees closely with their description.

The surface of the glabella is ornamented with a small number of large tubercles and a greater number of finer tubercles. The large tubercles were described by Raymond and Barton (1913, p. 530) as occurring in two rows "in a rough alignment" which "diverge toward the front." The arrangement of these tubercles is never symmetrical about the axis, and sometimes the two diverging rows are not clear, or most of the tubercles are on one side of the axis. They may be perhaps better described as occurring in a suboval area extending from just in front of the occipital furrow to immediately anterior to the third glabellar furrows, having a greatest width of about half that of the glabella at the second glabellar furrows. Within this area they are distributed as described, most numerous anteriorly, and almost without exception to one side of the median line. The large tubercles never occur close to or on the glabellar lobes. On the anterior slope of the glabella outside this area numerous slightly smaller tubercles are scattered, most numerous laterally, and rare near the median line. Still smaller tubercles are sparsely scattered everywhere over the glabella. The area between the tubercles is smooth.

The free and fixed cheeks within the borders are ornamented with irregular shallow pits, which pits have not been seen on the glabella. Three prominent tubercles on the fixed cheeks roughly in line parallel to the axis and just within the eye, the posterior tubercle being on the posterior margin.

The under surface of the test of *Ceraurus pleurexanthemus* was figured by Raymond and Barton (1913, pl. 2, fig. 7), but that of *C. aculeatus* Eichwald has been figured and described in much greater detail by Öpik (1937, pp. 100–102, pl. 18, fig. 41; pl. 17, fig. 7). The inner side of the glabella of *C. pleurexanthemus* shows the axial, glabellar

and occipital furrows as strong, wide ridges. The lateral extremities of the occipital furrow and the first pair of glabellar furrows are prolonged into stout appendifers, directed inwards as well as ventrally. The pair on the occipital ring are subtriangular in cross section, and thickened, those on the first glabellar furrows are rather bladelike and not thickened (pl. 73, fig. 38). The second and third glabellar furrows are not prolonged ventrally. The anterior pits, situated at the junction of the axial and preglabellar furrows, appear as low, subrounded eminences, and in the anterior face there is a moderately deep circular pit (pl. 73, fig. 40).

The anterior and lateral margins of the cephalon of *Ceraurus pleurexanthemus* are rolled under in the doublure, which is widest posterolaterally. The anterior branches of the facial sutures converge strongly and reach the margins at the axial furrows. In crossing the margins, they run obliquely forwards and cut the margin where it is vertical at points which are well within the projections of the line of the axial furrows. At these points they intersect with the epistomal suture and then run forwards, slightly inwards, and under as the connective sutures, and obliquely backwards over the doublure as part of the hypostomal suture, cutting the inner edge at points vertically under the axial furrows. The posterior branches of the facial sutures run in a gentle curve almost directly outwards from the eyes to the marginal furrows, then obliquely across the margin on to the doublure, where they turn abruptly and run transversely inwards to cut the inner edge vertically under the lateral terminations of the posterior marginal furrows. The posterior margin is without a doublure adjacent to the occipital ring, the margin being flexed sharply upwards to form a furrow behind the margin, which widens laterally. At about half the width the margin commences to be flexed under, and at this point the change in direction of bending forms an articulation socket (pl. 73, fig. 10). Laterally to these sockets the doublure widens gradually and is continuous with that of the fixed cheek. The genal spines form a continuous structure with these rolled margins.

Raymond (1920, p. 60) regarded the epistoma of *Ceraurus* as either entirely absent or very narrow, and does not indicate it in his reconstruction (1920, pl. 11), but it is clearly shown in *C. aculeatus* by Öpik (pl. 17, figs. 2, 3). It is evident when the separate hypostoma and free cheeks of *C. pleurexanthemus* are placed in correct association with the rest of the head shield, that an epistoma was present (text figs. 7, 8), but it has not been recognized in the material.

The hypostoma was figured but not described by Raymond and Barton (1913, pl. 2, fig. 7). The outline is suboval, the middle body strongly convex and undivided by a middle furrow; without maculae. The shallow lateral and posterior furrows separate the narrow convex border, which is widened very slightly at the posterior wings. The anterior furrow is shallow, the anterior border extremely narrow medianly, widening laterally and prolonged into the anterior wings. In dorsal view the lateral and posterior margins are flexed inwards, narrowest posteriorly, and extended in a dorsal direction as the posterior wings. The anterior wings are extended to a much greater degree dorsally and bent outwards in a curve. On the inner, anterior surface a strong boss appears in ventral aspect as a pit near the extremity (pl. 73, fig. 39). The middle body is ornamented by tubercles, which are large and well-spaced near the anterior furrow, and become smaller and closer set posteriorly. The lateral and posterior borders are finely tuberculate.

There is considerable variation in the proportions of the adult hypostoma, as shown in plate 73, figures 18–21, and by the dimensions.

Several cranidia differ in some details from those described above. The glabella is more strongly convex anteriorly and in consequence has a steeper frontal slope. The position of the eyes is the same, but the palpebral lobes rise very conspicuously higher in an upward and outward direction from the fixed cheeks. The ornament of the glabella and fixed cheeks is coarser. The largest tuberles on the glabella are conspicuous, and there are a few of equal size laterally on the frontal slope. The smaller tubercles scattered over the rest of the surface are relatively larger. One or two extra large tubercles occur on the fixed

cheeks and the posterior margin. These variations are conspicuous and always associated, the coarse ornament always being present with the more convex glabella and long palpebral lobes. The meaning of these variations is not clear, the rest of the cephalon being exactly like the other type. The variants do not seem to be confined to the cephala of a large size, specimens as small as that shown on plate 73, figures 12, 13 showing these features, while cephala as large as many of the variants do not show the unusual features.

A restoration of the thoracic segment of *Ceraurus pleurexanthemus* has recently been given by Størmer (1939, pp. 165–169, pl. 11), and the inner surface of the segments of *C. aculeatus* is described and illustrated by Öpik (1937, p. 100, pl. 18). The present material confirms in most details Størmer's restoration. The axial ring is more convex than Størmer showed it to be, and the appendifers are thick, curved, bladelike processes, directed inwards and downwards, and curving to point directly downwards at their extremities (the shape of the appendifers is clearly shown by Størmer's sections, pl. 73). In ventral aspect the elongated cross section of the appendifers is oblique to the transverse axis, the outer edge pointing outwards and a little forwards. Towards the extremity the cross section is a very narrow subtriangular shape, the sharper edge outwards (pl. 73, fig. 37). The conspicuous globular thickening at the extremities of the occipital and first pygidial appendifers has not been observed among the very few segments with unbroken appendifers. The articulating half ring is rarely preserved entire, but I have seen no indication of the thickened anterior margin such as Størmer shows on plate 11, figure a, but not in figures c, d.

The pleural spines show a variation from the anterior to the posterior end of the thorax. The first pair are directed straight outwards, and taper more rapidly than those of succeeding segments. Each successive segment has the spines curved increasingly strongly backwards, the last pair being short, broad, and pointing directly backwards (pl. 73, figs. 33, 36). All the pleural spines are bent gently ventrally.

The pygidium is composed of four segments. The inner surface shows four pairs of appendifers (pl. 73, fig. 35; cf. also *C. aculeatus*, Öpik 1937, p. 100, pl. 17, fig. 7). The first pair are directed downwards and inwards, triangular in cross section, and thickened at the extremity, and are similar to the appendifers of the occipital ring. The second pair arise at the continuation of the articulating furrow just outside the faint axial furrows, and are triangular plates, bluntly pointed, and bent over forwards. The third pair are similarly shaped, much smaller, a little farther outside the axial furrows, and consequently obliquely placed relative to the other pairs owing to the sharp backward bend of the transverse furrows. The fourth pair are low, rounded.

The doublure is wide, sharply flexed, and thus with a V-shaped cross-section, the V becoming deepest posteriorly. The inner edge is posteriorly extended, with a curved margin, into the axial lobe, and in posterior view the overhanging margin is slightly indented (pl. 73, fig. 35). The doublure is ornamented with closely set tubercles except posteriorly near the inner edge.

Development.—The smallest cephala in the material are 1.1 mm. in length. They are in no essential way different from the adult. The smallest hypostoma are proportionately broader and less convex.

The smallest pygidia are subtriangular in outline, having four segments anterior to the segment with the prominent, long, pleural spines. The two most anterior of these segments have the diagonal pleural furrow. The pleural spines of the anterior segment are moderately long, curved, and directed outwards and backwards, ornamented with short spines. The pleural spines of the next three segments are progressively shorter and more backwardly directed. The short part of the pygidium behind the fifth segment is bent down, with two segments demarcated on the rachis by shallow furrows. The anterior edge of the axial ring of the first segment carries the articulating half ring. On the inner surface on the posterior edge the posterior doublure and articulating half ring of the second segment are developed as a single structure, apparently as a horizontal forwardly directed fold continuous with the articulating furrow of the second segment. A similar,

shorter development of the articulating half ring and posterior doublure between the second and third segments (pl. 73, fig. 28, text-fig. 11). The sixth segment has a faint boss at the junction of the axial and articulating furrows on the inner surface. The fifth segment has a more distinct boss, the fourth a distinct small appendifer just within the axial furrow. With each more anterior segment the appendifer moves in from the axial furrow and is more strongly developed. On the first four segments the doublure is narrow and curled over. It widens perceptibly at the fifth, but is gently rolled as compared with the adult.

Pygidia of increasing size have progressively one segment less in front of the segment with the main pleural spines. The development of the articulating half ring and posterior doublure and of the appendifers is seen as before (pl. 73, figs. 29, 32, text figs. 12, 13). The smallest pygidia having the long pleural spines on the anterior segment bearing the long pleural spines, are very similar to the adult. The only subsequent changes are that the doublure becomes strongly rolled under, and the shallow posterior indentation of the doublure more marked.

The anterior segment of the transitory pygidium appears to become released into the thorax by the development of a suture along the rib furrows and the anterior edge of the fold which forms the posterior doublure and the articulating half ring of the next segment. It might be expected that this separation would take place during ecdysis, but in the specimen shown in plate 73, figure 32 and text figure 13, the suture is partly developed along the rib furrow on the right of the pictures, and is partly developed between the posterior doublure and the articulating half ring.

Dimensions.—The sagittal lengths and the maximum widths of several specimens of *Ceraurus pleurexanthemus* are enumerated below. The length and width of the cephalon and the length and width of the glabella of 13 individuals are, respectively, 1.1, 2.8, 0.9, 1.0 mm.; 1.1, 2.6, 0.9, 1.0 mm.; 1.5, 3.6, 1.2, 1.3 mm.; 1.5, 3.3, 1.2, 1.3 mm.; 1.8, 2.4, 1.0, 0.9 mm.; 2.7, 6.3, 2.4, 2.3 mm.; 2.9, 7.0, 2.3, 2.5 mm.; 3.1, 6.4, 2.5, 2.1 mm.; 4.4, 10.5, 3.4, 3.3 mm. (pl. 73, fig. 3); 8.5, 24.0, 6.6, 7.1 mm. (pl. 73, fig. 4).

The length and width of the hypostoma of 14 individuals are, respectively, 0.8, 1.1 mm.; 1.2, 1.5 mm.; 1.3, 1.5 mm.; 1.3, 1.4 mm.; 1.9, 2.2 mm.; 2.1, 2.3 mm.; 2.2, 2.7 mm.; 2.5, 1.7 mm.; 2.9, 2.2 mm.; 2.9 3.4 mm.; 3.6, 4.3 mm. (pl. 73, fig. 18); 3.9, 4.3 mm.; 4.7, 5.6 mm.; 4.8, 4.8 mm. (pl. 73, fig. 20).

The length and width of 12 pygidia are, respectively, 0.7, 1.3 mm. (pl. 73, fig. 29); 0.8, 1.1 mm. (pl. 73, fig. 22); 0.8, 1.0 mm.; 0.8, 1.8 mm. (pl. 73, fig. 24); 1.0, 1.4 mm. (pl. 73, fig. 23); 1.1, 1.8 mm. (pl. 73, fig. 31); 1.3, 2.2 mm.; 1.3, 2.2 mm.; 1.6, 3.2 mm.; 1.6, 3.2 mm.; 1.7, 3.2 mm.; 2.8, 5.5 mm.

Family ODONTOPLEURIDAE Burmeister, 1843

Genus DIACANTHASPIS Whittington, n. gen.

Genotype, *Diacanthaspis cooperi* Whittington, n. gen., n. sp.

Glabella a little wider than long, with two pairs of suboval lateral lobes, the posterior pair the larger; the median lobe wider than the lateral lobes. Occipital ring long, a very prominent pair of marginal spines; occipital lobes small, faint. The eyes situated near the posteroaxial corner of the cheeks; facial sutures not fused. Genal spine curved, occurring at the posterolateral angle of the cephalon as a projection of the rolled margin of the free cheeks. Cephalon ornamented with numerous short spines in symmetrical arrangement.

Number of thoracic segments unknown. The axial ring with a conspicuous pair of spines, the anterior pleural band with a short marginal spine, the posterior band with a long marginal spine. Other short spines in symmetrical arrangement on the axial rings and pleurae.

Pygidium of three segments. The three segments of the rachis with paired spines. The pleural lobes with a prominent pair of upwardly directed spines situated opposite the second segment of the rachis. Margin with 12 spines of equal length, other short spines on the rachis and pleural lobes.

Discussion.—Two species of odontopleurid have been described from the Trenton, the first by Hall in 1847 (pp. 240–241, pl. 64, figs. 4a–f), the specimens coming from the Bay of Quinta, Lake Ontario,

Canada. The type of this species, *Leonaspis? trentonensis*, is illustrated (pl. 74, figs. 31–34) as well as two other specimens, from the Trenton at Trenton Falls, New York, (pl. 74, figs. 35–37). The glabella of this species differs from that of *Diacanthaspis cooperi* n. gen., n. sp. in outline, in the relative proportions of the first and second lateral glabellar lobes and in possessing the small third lateral lobes. The occipital ring appears to have the faint lateral lobes, but does not have the stout pair of marginal spines. The rachis of the thorax and pygidium has no paired spines, the posterior pleural bands of the thorax are elevated laterally, the pygidium is without the upwardly directed pair of spines, and, though the margin bears 12 spines, one pair is stouter and longer. I have therefore placed Hall's species tentatively in the genus *Leonaspis* R. and E. Richter, 1917.

Walcott (1879, p. 69) described the species "*Acidaspis*" *parvula* from the Trenton of Trenton Falls. The holotype and paratypes have never been prepared and are not well preserved. Material of this species appears to be rare, the common odontopleurid in material from Trenton Falls being apparently Hall's species. The types however, show the prominent paired spines on the glabella, occipital ring, and the rachis of the thorax and pygidium. The first and second lateral lobes are of subequal size, and the eyes are situated near the posteroaxial corners of the cheeks. It is probable, therefore, that Walcott's species should be placed in the new genus *Diacanthaspis*, but a decision on this point awaits the redescription of "*A.*" *parvula*.

The Ordovician genus *Primaspis* R. and E. Richter, 1917, shows some resemblances to *Diacanthaspis*, n. gen., but the glabella differs in proportions, the third lateral lobes are present, the paired spines are present on the occipital ring but not on the rachis of the thorax and pygidium, and the pygidium possesses the elongated pair of marginal spines.

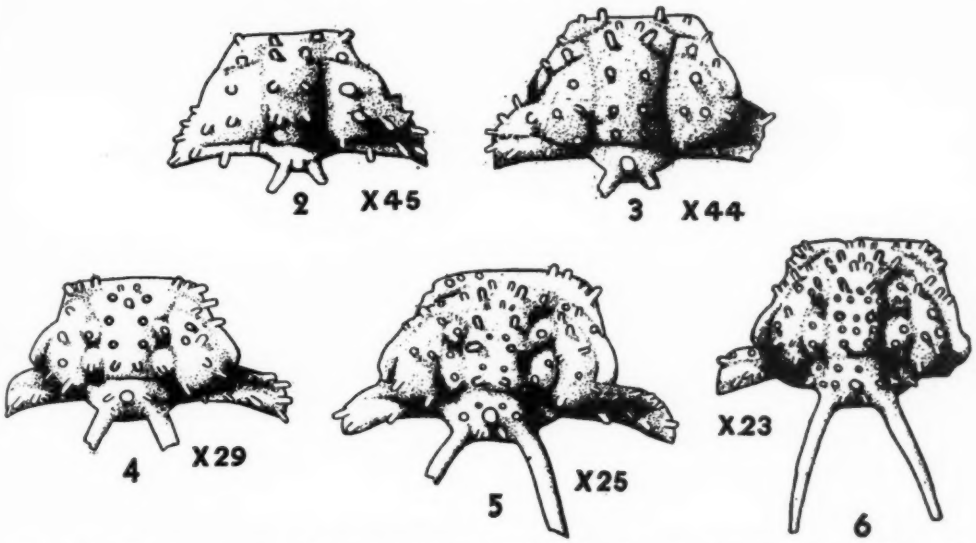
I have examined the types of the Chazy genus *Onchaspis* Raymond, 1925, and also some silicified specimens belonging to this genus. The glabella and pygidium are quite different from those of *Diacanthaspis*, n. gen.

The most recent writings on the *Odontopleuridae*, by Reed (1925), Warburg (1934), Öpik (1937), Whittard (1938), indicate the confusion which prevails in the nomenclature of this group. A comprehensive revision of the known genera and species of this family is needed, and this would enable a grouping into subfamilies to be made. The importance of the spines in the classification of the family might also be estimated. My observations on the ontogeny of *Diacanthaspis*, n. gen., indicate that the paired spines occur on the axial portion of every segment of the dorsal surface, and are thus fundamental in the structure of the trilobite. Other genotype species appear to possess very different arrangements of the spines.

DIACANTHASPIS COOPERI Whittington, n. gen., n. sp.

Plate 74, figures 1–30; text figures 2–6

Outline of cephalon subsemicircular. Glabella a little longer than wide, sides subparallel, gently convex transversely, standing a little higher than the fixed cheeks, sloping steeply down anteriorly in a convex curve. The anterior lobe is suboval in outline and forms a continuous structure with the elongate nearly parallel-sided median part of the glabella. Flanking the median part are the two pairs of lateral lobes, oval in outline, elongate axially, and defined by the two pairs of glabellar furrows, which are shallow and directed obliquely backwards, and by the shallow lobe grooves connecting the inner ends of the glabellar furrows with each other and the occipital furrow. Occipital ring long, about one-third the length of the glabella, the margin curved strongly backwards and bearing near its lateral extremities a pair of long, stout, diverging spines, directed almost in the horizontal plane. There are two short, thin, marginal spines between these, and a short, thick, median spine. A pair of small, circular occipital lobes at the lateral extremities posterior to the first glabellar lobes. These occipital lobes are most easily seen on the ventral surface. Occipital doublure suboval in outline, reaching forward nearly to the occipital furrow. Preglabellar furrow shallow, preglabellar field exceedingly narrow, especially axially, and flexed down along the



FIGS. 2–6—The development of the cranidium of *Diacanthaspis cooperi*, n. gen. n. sp. The axial spines of the glabella and preglabellar field are indicated in heavier outline. Drawn from the originals of plate 74, figures 1, 2, 3, 8, 6, respectively. Arranged in order of increasing size. Magnifications given are approximate.

straight margin. Axial furrows shallow, directed obliquely inwards to the lateral terminations of the second glabellar furrows, then curving out around the glabellar lobes, and in behind the first lobes.

The eyes are situated far back, opposite the first glabellar lobes, and are the highest points on the cephalon. The anterior branches of the facial sutures converge very slightly, and the posterior branches run outwards and backwards, so that the fixed cheeks are roughly L- and reversed L-shaped. Anterior to the eye sloping gently forward in a convex curve, and crossed by the strong eye ridges, which run from the axial furrows opposite the anterolateral edges of the glabella to the anterior edges of the palpebral lobes. Outside the eye ridges a furrow, continuous with the preglabellar furrow. Posteromedially to the eyes the fixed cheeks descend steeply in a convex curve to the margin and are vertical adjacent to the axial furrows, where no posterior margin or posterior marginal furrow is distinguishable. Posterolaterally to the eyes short, the posterior marginal furrow curving in from the margin and running outwards, the posterior margin narrow, convex, with extremely narrow doublure.

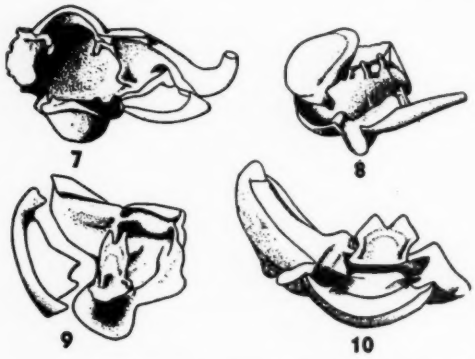
Free cheeks subtriangular in outline, sloping steeply down to the margin in a concave curve. Margin rolled, doublure narrow, with a row of spines, longest posteriorly, directed outwards, and forming a continuous structure with the long, curved genal spine.

Hypostoma subquadrate in outline, about as long as wide, middle body gently convex and borders narrow. The middle furrow commences at the broad, shallow pit situated at the anterolateral margins of the middle body and reaches back in a curving course to about two-thirds the length. Anterior border narrow, bent over dorsally, small pointed anterior wings. Lateral borders narrow, carrying the small posterior wings, opposite which the lateral furrows are conspicuously deeper. Posterior border narrow, curved. Doublure narrow, except at the wings, where it is drawn out dorsally in a triangular tongue.

Except in the furrows the cephalon is coarsely ornamented with well-spaced, short spines, the spaces between occupied by very small tubercles. The margin of the free cheeks bears the horizontal, outwardly directed spines, on which there are small, scattered tubercles, and the preglabellar

field is without marginal spines. The long genal and occipital spines are tuberculate also.

Thorax not well known, only a few axial segments among the material. Axial ring very convex, with broad articulating furrow. A short median spine directed upwards and a pair of stouter spines beside and a little behind, directed upwards and a little backwards, these three spines correspondingly arranged to those on the occipital ring, but the pair directed nearly upwards instead of horizontally. Three or four additional spines laterally. Pleurae flat, divided by the shallow furrow into a narrow anterior band and a wider, convex posterior band. The anterior band with about three short spines and a short anterior pleural spine, which bears secondary spines, directed outwards. The posterior band with three or four stouter spines and a long, thick, slightly curved posterior pleural spine directed outwards and backwards, more strongly backwards in the more posterior segments. The posterior pleural spine overlies the anterior pleural spine of the succeeding segment. The areas between the spines on the anterior and posterior pleural bands covered with small tubercles. On the anterior extremities of the pleurae an articulating process, and a corresponding socket on the posterior extremities.



FIGS. *7–10*—Ventral views of the cephala of *Ceraurus pleurexanthemus* and *Flexicalymene senaria*. *7*, Posterior view of the ventral surface of an incomplete cranidium, free cheek, and hypostoma of *Ceraurus pleurexanthemus*, placed loosely together in suggested relative positions during life. *8*, Incomplete cranidium and hypostoma of the same species, similarly placed, lateral view of ventral surface. *9*, Lateral view of the ventral surface of an incomplete cranidium, free cheek, and hypostoma of *Flexicalymene senaria*, placed loosely together in suggested relative positions during life. *10*, The same, similarly placed, anterior view of the ventral surface. Drawings made from the specimens mounted together in the positions shown. *7*, Lighting from the west; *8*, *9*, from the northwest; *10*, from the northeast.

Pygidium short, subtriangular in outline. Rachis strongly convex. Two distinct segments with the median and paired spines as on the axial segments, and on the posterior slope three much smaller spines similarly arranged suggest a third segment. Two additional spines on each side of the first two annulations. Axial furrows indistinct. Pleural lobes flat, pleural furrows of first segment weakly indicated. Twelve strong radiating spines of almost equal length equally spaced around the margin. Three short spines on the anterior pleural band of the first segment, two on the posterior band. Between the inner pair of these latter and the base of the fourth pair of marginal spines a stout spine directed upwards and slightly backwards. The position of the first two pairs of marginal spines indicates that they are the homologues of the anterior and posterior pleural spines of the axial segments, and the presence of 12 marginal spines further suggests that the pygidium consists of three fused segments. The anterior margin with the articulating half ring and articulating processes at the lateral extremities. Doublure curled evenly under, widest posteriorly and narrowing gradually laterally. The posterior pleural spines of the last axial segment overlie the first two marginal spines. The spaces between the spines covered with fine tubercles, and the marginal spines with tubercles also.

Development.—THE CEPHALON: The smallest cranidia known referable to this species are 0.4 mm. in length (pl. 74, fig. 1, text fig. 2). Outline subtrapezoidal. Glabella longer than wide, convex at the rounded anterior end, the axial furrows shallow, almost straight, and converging slightly posteriorly. A pair of faint, short, shallow, glabellar furrows situated opposite a point immediately posterior to the second axial spines (see below). Preglabellar furrow shallow, ill-defined. Preglabellar field extremely narrow, especially axially, margin straight. A pair

of spines on the preglabellar field and three pairs on the glabella, which are arranged in two longitudinal lines converging posteriorly. I propose to refer, for brevity, to these spines as the third, fourth, fifth, and sixth axial spines, commencing numbering forwards with the paired spines on the occipital ring.

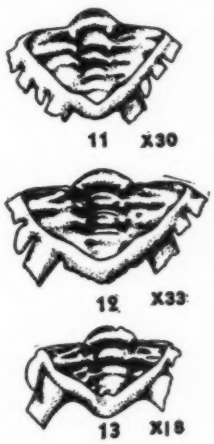
The occipital ring strongly convex, prolonged backwards, margin curved, and bearing two stout diverging spines (the first axial spines). The median spine is short and thick. Occipital doublure reaching forward to about two-thirds the length of the ring.

Fixed cheeks triangular in outline, strongly convex, sloping gently forwards and more steeply posteriorly. Eyes situated opposite a point a little in front of half the length of the glabella and not at the highest point, which is directly opposite the third axial spines. Broad eye ridges run obliquely from the axial furrows opposite the fifth axial spines to the anterior margin of the palpebral lobes. A pair of spines on the preglabellar field anterior to the fixed cheeks. Two pairs of spines on the fixed cheeks, a pair situated on the eye ridges opposite the fifth axial spines, a pair opposite the fourth axial spines, and two pairs opposite the third axial spines. The spines thus form transverse rows across the cephalon, the spine rows, the first being across the posterior margin and occipital ring, the second is not yet present, the third and fourth across the glabella and fixed cheeks, the fifth across the glabella and eye ridges, the sixth across the preglabellar field. A further pair of spines occurs in the posteroaxial corners of the fixed cheeks. Posterior marginal furrows shallow and indistinct laterally, absent axially. Posterior margin convex with about four spines. Doublure very narrow. The anterior branches of the facial sutures converge forwards, and the posterior branches diverge backwards and form practically a straight lateral boundary to the fixed cheeks.

Free cheeks unknown.

A slightly larger cranidium (pl. 74, fig. 2, text fig. 3), differs but slightly from the previous. The glabella is a little more convex, the second glabellar furrows are now present, short and shallow, and situated immediately posterior to the fourth axial spines. The second glabellar furrows a little more distinct.

The eyes are situated just behind a point opposite the fourth axial spines. The posterior branches of the facial sutures diverge more strongly and are curved, and thus the outline of the cranidium is less markedly trapezoidal. An additional pair of spines in the third, fifth and sixth spine rows. The backward movement of the eyes gives a pronounced curve, convex forwards, to the fifth spine row, and the third and fourth spine rows are similarly curved, but less strongly. Two new pairs of small spines on the glabella, one anterior to the fifth axial spines, the other posterior to the third axial spines. This latter pair is the second pair of axial spines, the last to appear. They are opposite the first glabellar lobes. The pair of spines in the posteroaxial corners of the fixed cheeks, opposite the second axial spines, delineate the second spine row.



FIGS. *11–13*—The ventral surface of three transitory pygidia of *Cerarurus pleurexanthemus*. The specimens are part of the developmental series, and have respectively four, two, and one segments anterior to that with the main pleural spines. The latter is the anterior segment of the true pygidium. The development of the appendifers, the articulating half ring, and the posterior doublure is shown. Drawn from originals of plate 73, figures 28, 29, and 32 respectively.

Larger cranidia, of length 0.7 mm. (pl. 74, fig. 3, text fig. 4), have the glabella with the anterior lobe distinctly widest, the posterior part with the subparallel sides and the two

pairs of glabellar lobes small and faintly outlined. The relative position of the third and fourth axial spines and the second glabellar furrows remains the same, but the anterior lobe is now considerably less in length than the rest of the glabella, whereas in smaller cephala it was approximately the same length. The axial furrows are a little deeper and swing in behind the first glabellar lobes into a pair of broad, deep, subcircular pits. Behind these pits the convex extremities of the occipital ring form a continuous structure with the posteroaxial corners of the fixed cheeks, undivided by any distinct axial furrows.

The eyes are situated a little farther back and in from the margin, opposite the first glabellar furrows. The lateral margins of the fixed cheeks are thus indented, the anterior branches of the facial sutures converging less strongly, the posterior branches very strongly divergent and curving to cut the posterior margin. The highest point on the fixed cheeks posteroaxially to the eyes. The posterior margin is now absent behind the ridge uniting the occipital ring and fixed cheeks but is present and widens laterally, demarcated by a shallow furrow.

Free cheeks subtriangular in outline, sloping almost vertically down from the eye in a concave curve and almost flat laterally, with a wide, rolled margin, which is extended posterolaterally into the curved genal spine. The margin with closely spaced spines radiating outwards, short anteriorly, increasing in length posteriorly, and the concave border with a few more widely spaced spines directed upwards and outwards. One additional pair of spines in the sixth spine row. The first median spine appears on the glabella in quincuncial arrangement with the fourth and fifth axial spines. A spine appears on each of the glabellar lobes. The third, fourth, and fifth spine rows more strongly curved backwards with the new position of the eye. Surface of the glabella between the spines coarsely tuberculate.

Cephala of length 0.9 mm. are quite similar to the adult (pl. 74, fig. 4, text fig. 5). The glabella is nearly parallel sided, the lateral lobes more conspicuous. The anterior lobe is now approximately one-half the length of the rest of the glabella. The axial furrows are shallow, but the glabellar furrows are deep. Posteriorly to the first glabellar lobes the junction of the occipital and axial furrows forms the pair of broad, deep pits noted above, which are now deeper. Behind them the more convex occipital ring is connected by lower, narrower, convex marginal ridges to the posteroaxial angles of the fixed cheeks.

The margin of the preglabellar field is now gently curved. The eyes are situated a little

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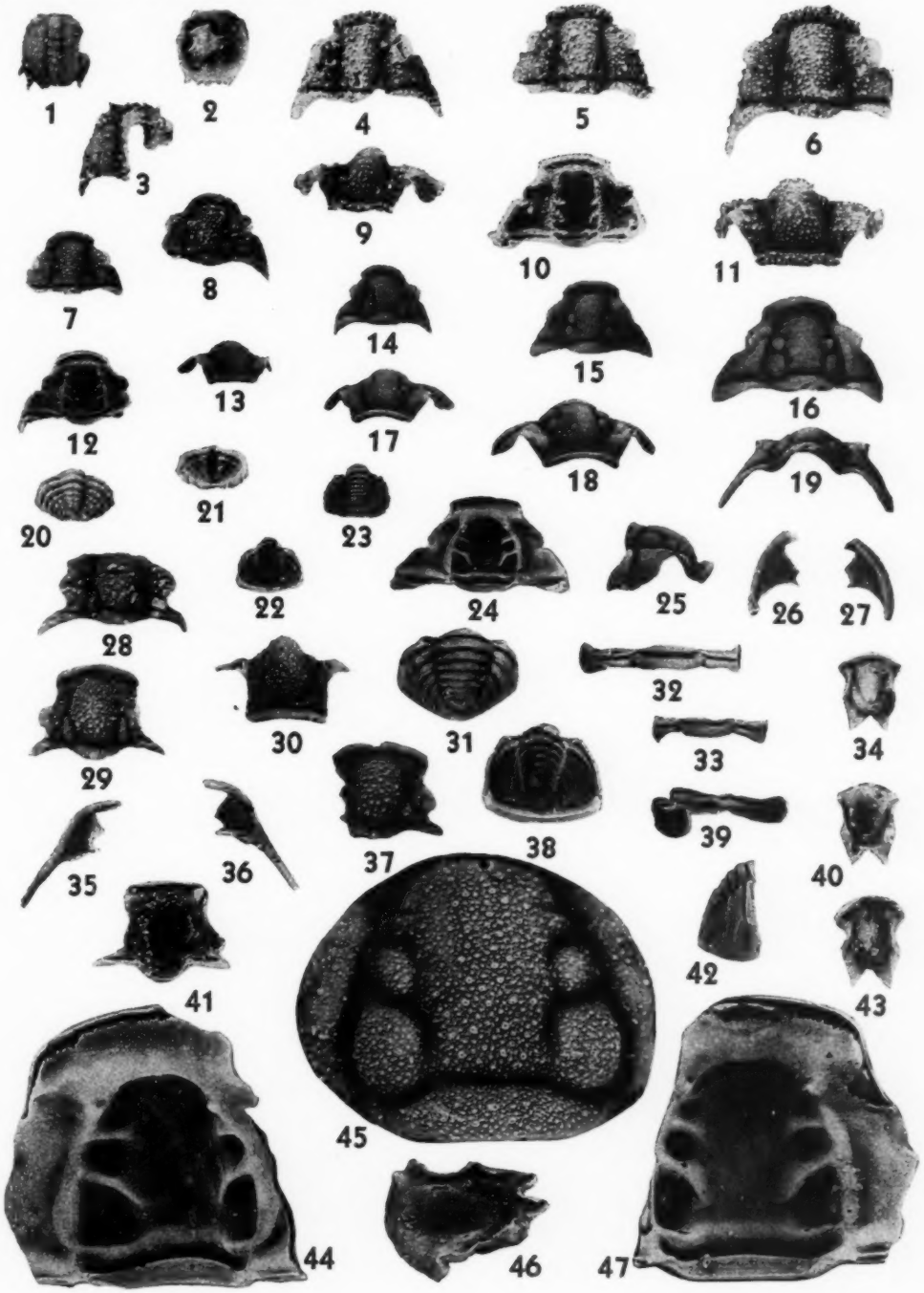
EXPLANATION OF PLATE 72

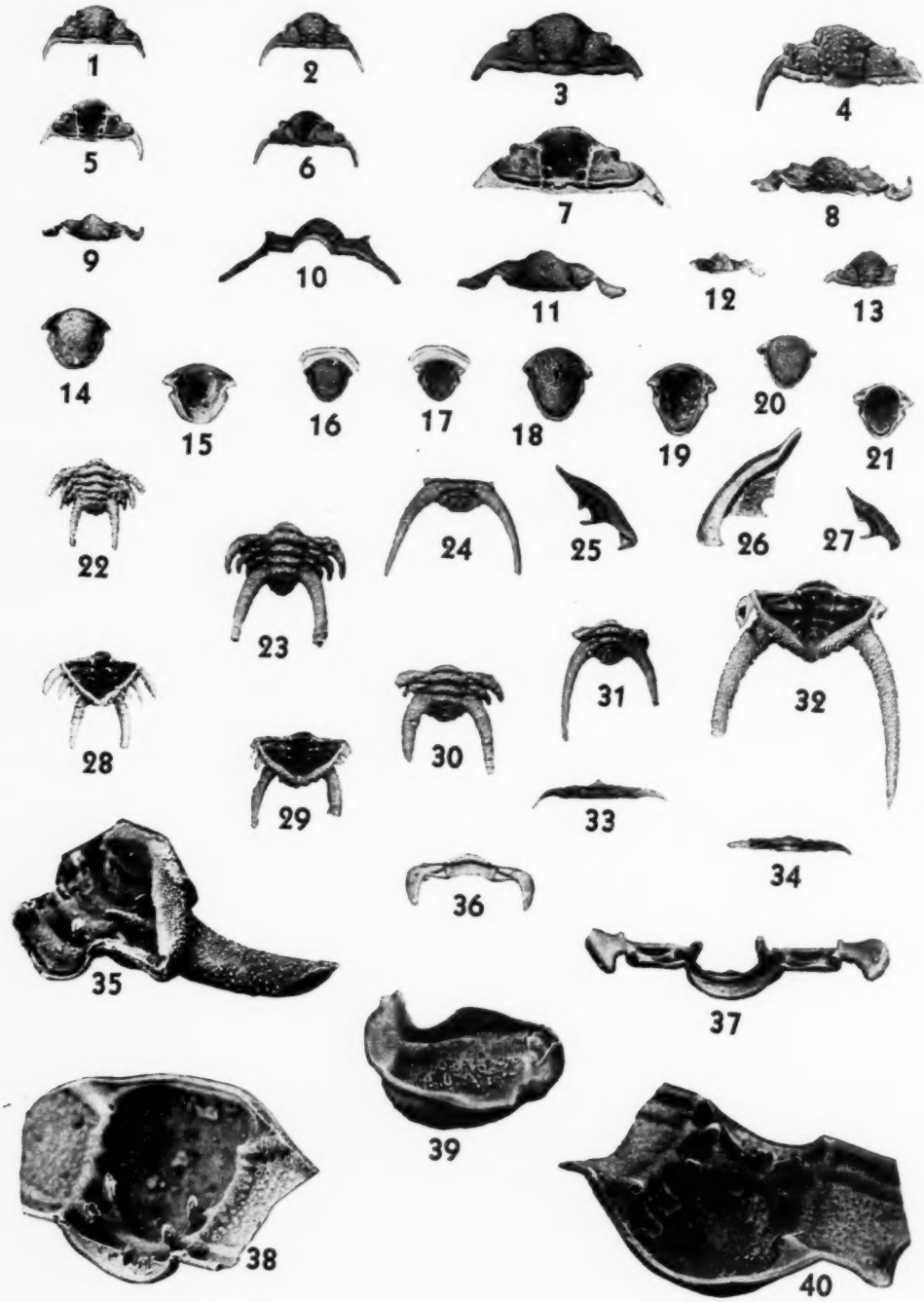
Untouched photographs of specimens from 2½ miles NNE. of Spring Hill, Va., in the United States National Museum.

FIGS. *1–27, 31–34, 38–40, 42–47—Flexicalymene senaria* (Conrad). *1*, Protaspis, dorsal view, ×15. *2*, Protaspis, ventral view, showing slightly displaced hypostoma, ×15. *3*, Meraspid cranidium, dorsal view, ×15. *4, 9*, Cranidium, dorsal and anterior views, ×10. *5, 10*, Cranidium, dorsal and ventral views, ×10. *6, 11*, Cranidium, dorsal and anterior views, ×10. *7*, Cranidium, dorsal view, ×5. *8, 12*, Cranidium, dorsal and ventral views, ×5. *13, 14*, Cranidium, anterior and dorsal views, ×3. *15, 17*, Cranidium, dorsal and anterior views, ×3. *16, 18, 19, 24, 25*, Cranidium, dorsal, anterior, posterior, ventral, and lateral views, ×2. *20, 21*, Transitory pygidium, dorsal and ventral views, ×10. *22, 23*, Pygidium, ventral and dorsal views, ×5. *26, 27*, Free cheek, ventral and dorsal views, ×2. *31, 38, 42*, Pygidium, dorsal, ventral, and lateral views, ×2. *32, 39*, Anterior thoracic segment, dorsal view and lateral view of ventral surface, illuminated from the northeast, ×2. *33*, Posterior thoracic segment, dorsal view, ×2. *34, 40*, Hypostoma, ventral and dorsal views, ×10. *43*, Hypostoma, ventral view, ×5. *44*, Portion of cranidium, ventral view, showing anterior pits, glabellar furrows, posterior doublure, ×5. *45*, Portion of cranidium, dorsal view, showing openings in tubercles, ×10. *46*, Hypostoma, anterolateral view of dorsal surface, ×5. *47*, Part of cranidium, ventral view, showing canal openings in glabella, preglabellar field, and fixed cheeks, ×5. (p. 493)

FIGS. *28–30, 35–37, 41—Otarion* sp. *28*, Incomplete cranidium, dorsal view, ×15. *29, 30, 41*, Cranidium, dorsal, anterior, and ventral views, ×5. *35, 36*, Free cheek, dorsal and ventral views, ×5. *37*, Incomplete cranidium, dorsal view, ×5. (p. 512)



Whittington, Trenton Trilobites



Whittington, Trenton Trilobites

farther backwards and inwards, on the highest point of the fixed cheeks, and the latter now slope more steeply posteriorly, almost vertically as in the adult. The posterior margin is more convex, and the posterior marginal furrow deeper. The free cheeks (pl. 74, fig. 18) are as before, with about six spines on the border and 12 on the margin. The doublure projects beyond the anterior margin under the preglabellar field.

The ornament of the cephalon appears less coarse owing to the increased size and the presence of some new spines. Paired spines appear on the glabella outside the fifth axial spines, between the fourth and fifth, and third and fourth, and second and third axial spines. A second spine is present on the first lateral lobes. A new pair of spines is present in each of the fifth and sixth spine rows, and apparently in the third. On the occipital ring there is now a small pair flanking the median spine and on the margin between the main pair and anterior to the median spine. The surface of the test between the spines is tuberculate.

The next largest cephala, of length 1.0 mm. (pl. 74, fig. 6, text fig. 6), have the glabella distinctly more convex. The occipital ring is also a little more convex and may now clearly be subdivided. The central part, bearing the main spines, descends steeply laterally along lines which are continuous with the outer edges of the spines. The lateral extremities are thus depressed, and the first glabellar lobes and the fixed cheeks slope steeply down to them and are bounded from them by the shallow occipital and axial furrows. A very shallow furrow separates the convex median part from the depressed lateral extremities, which are thus the faintly outlined occipital lobes. They have developed in the depressed region present in smaller cephala immediately posterior to the first glabellar lobes.

The rest of the cephalon appears much as before, the ornamentation is relatively a little less prominent, but there are few new spines. On the glabella two pairs appear flanking the pairs between the fourth and fifth, and third and fourth, axial spines. Two new median spines appear, and additional spines on the glabellar lobes. A small spine appears on the occipital lobes.

Cephala of increasing size up to the adult show very little further change. There is a general increase in convexity, resulting in a steeper anterior slope to the glabella and a steeper posterior slope of the fixed cheeks behind the eye. The number of short spines forming the ornamentation increases greatly, On the glabella this can be seen to be by intercalation of new pairs of spines or single median spines among those already present. Especially clear is the arrangement of new spines appearing on the occipital ring. A small median spine appears in front of the main one or, in some specimens, a pair of spines close together, flanked by three further pairs. The main median spine is already flanked by a pair, and new ones appear within and without these. Additional spines appear on the glabellar lobes and also

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EXPLANATION OF PLATE 73

Untouched photographs of specimens from 2½ miles NNE. of Spring Hill, Va., in the United States National Museum.

FIGS. *1–40*—*Ceraurus pleurexanthemus* Green. *1, 5, 9*, Cranidium, dorsal, ventral, and anterior views, ×5. *2, 6*, Cranidium, dorsal and ventral views, ×3. *3,7, 10, 11*, Cranidium, dorsal, ventral, posterior and anterior views, ×2. *4, 8*, Cranidium, dorsal and anterior views, ×1. *12, 13*, Cranidium, anterior and dorsal views, ×2. *14, 15*, Hypostoma, ventral and dorsal views, ×10. *16, 17*, Hypostoma, ventral and dorsal views, ×5. *18, 19*, Hypostoma, ventral and dorsal views, ×2. *20, 21*, Hypostoma, ventral and dorsal views, ×2. *22, 28*, Transitory pygidium, dorsal and ventral views, ×10. *23*, Transitory pygidium, dorsal view, ×10, *24*, Pygidium, dorsal view, ×3. *25*, Free cheek, dorsal view, ×2. *26*, Free cheek, ventral view, ×2. *27*, Free cheek, dorsal view, ×5. *29, 30*, Transitory pygidium, dorsal and ventral views, ×10. *31, 32*, Transitory pygidium, dorsal and ventral views, ×5, ×10. *33, 34*, Anterior thoracic segment, dorsal and ventral views, ×1. *36, 37*, Posterior thoracic segment, dorsal view, ×2, posteroventral view, ×5. *35*, Pygidium, anterolateral view of ventral surface, showing appendifers, ×5. *38, 40*, Part of cranidium, posterolateral view of ventral surface showing appendifers, anterior view showing anterior pits, ×5. *39*, Hypostoma, anterolateral view of dorsal surface, ×5. (p. 498)

on the now more distinct occipital lobes. It is difficult to trace arrangement in the spines on the fixed and free cheeks, but they become more numerous and are evenly spaced from each other. Over the cephalon the spines are thus in an irregular quincuncial arrangement, with a tendency to be in transverse lines across the glabella, and on the fixed cheeks beside and in front of the eyes in curving lines subparallel to the eye ridges.

THE PYGIDIUM: The smallest pygidium in the material (pl. 74, fig. 11) is of a size which suggests that it may belong to the smallest cephalon described. The rachis is convex, narrowing posteriorly, and divided by ring furrows into three rings, each of which bears a pair of spines. The pleurae of the first segment are divided into the anterior and posterior bands, the former with a very short marginal spine, the latter with a long, slightly curved marginal spine directed backwards and a little outwards. Near the extremities of the posterior bands a short spine directed upwards. The margin of the pygidium posteriorly to the first segment bears two pairs of long spines, the first pair directed backwards and inwards, the second more strongly inwards and shorter. These are presumably the marginal spines of the posterior pleural bands of the second and third segments. Laterally on the second segment a pair of short spines directed upwards, corresponding to those on the first segment. The six marginal spines are ornamented with small spines. The margin of the pygidium is curled under in a narrow doublure.

The next largest pygidia (pl. 74, fig. 12) are similar in appearance, the rachis having three distinct segments with paired spines, and the margin with three prominent pairs of posterior pleural spines and the anterior pleural spine of the first segment. A new paired spine appears on the posterior pleural bands, directed upwards and situated within the lateral paired spines noted above. On the rachis a very small pair of spines at the posterior extremity presumably indicates a fourth segment, which supposition is borne out by the presence on one specimen of an additional pair of very small marginal spines posteriorly.

Slightly larger pygidia exhibit four segments distinctly, the fourth pair of spines on the rachis and the margin being more prominent. The short spines of the anterior pleural bands of the first two segments may be seen, directed backwards and placed lower down on the margin than the larger posterior spines.

The next largest pygidia differ in many respects and are very similar to the adult. It is proportionately shorter, and the rachis has two pairs of spines on the two rings. A second pair outside the first pair. The margin bears 12 evenly-spaced spines of about equal length, directed progressively less strongly outwards posteriorly. These spines are ornamented with numerous small spines, and presumably represent the marginal spines of the anterior and posterior pleural bands of three segments. The prominent pair of long spines, directed upwards and a little backwards, are now developed and situated opposite the second axial ring. The margin is much more strongly rolled under. With increasing size the pygidium alters little after this stage. A third pair of spines appears on the rachis, and median and additional flanking spines on the first two rings. Small spines also appear on the pleurae, and low ridges are developed connecting the first axial ring with the prominent lateral spines.

DISCUSSION OF THE DEVELOPMENT: The drawings (text fig. 2–6) summarize the changes which take place in the cranidium during development. The outline of the glabella does not alter very markedly. The first glabellar furrows are first present, then the second appear, and the lateral lobes gradually take shape. The proportional decrease in length of the anterior lobe relative to the rest of the glabella, from one-half to one-third, is notable. It seems to indicate a relatively more rapid growth of the posterior part of the cephalon, and concomitantly there is a backward migration of the eyes and an increase in convexity. In the smallest cephala the posterior border and marginal furrows are almost in a straight line with the occipital ring and furrow, but with this hypertrophy posteriorly the occipital ring increases greatly in convexity and length, the fixed cheeks acquire a very convex slope posteroaxially, and the posterior margin is apparently squeezed out adjacent to the occipital ring. The extremities of the latter are depressed, and on them

the small, ill-defined occipital lobes develop.

The arrangement of the spines on the cranidium indicates that, if not median, they are symmetrically in pairs. The smallest cranidium is notable in having five transverse rows of spines, in which are included the axial spines. The occipital ring bears a very prominent pair of spines, and the axial ring of every segment of the thorax and pygidium also bears a pair of spines in like position. During development median spines and flanking pairs of spines appear on the axial rings, and pairs of spines on the pleurae of the thorax and pygidium. The axial spines and spine rows of the glabella, preglabellar field and fixed cheeks may therefore perhaps be the homologues of the spines on the occipital segment and the segments of the thorax and pygidium.

The development of the thorax is not known. The pygidium exhibits a notable change in its growth when it becomes stable at three segments, possesses the 12 marginal spines of equal length, and develops the upwardly directed pair of spines on the pleural lobes. This change may be that from the transitory to the true pygidium, and the anterior segment of the smaller pygidia resembles the thoracic segments in having the short spines on the anterior pleural bands and the long spines on the posterior pleural bands.

Dimensions.—The sagittal length and maximum width of several individuals of *Diacanthaspis cooperi* are enumerated below. The length and width of the cephalon and the length and width of the glabella of 11 specimens are, respectively, 0.4, ?, 0.3, 0.2 mm. (pl. 74, fig. 1); 0.5, 0.8, 0.3, 0.2 mm. (pl. 74, fig. 2); 0.7, 1.5, 0.5, 0.5 mm. (pl. 74, fig. 3); 0.8, 1.8, 0.5, 0.6 mm.; 0.8, 1.6, 0.5, 0.6 mm.; 0.9, 1.7, 0.5, 0.6 mm. (pl. 74, fig. 4); 1.0, ?, 0.7, 0.5 mm. (pl. 74, fig 6); 1.4, 2.8, 0.9, 1.0 mm.; 1.8, 3.6, 1.1, ? mm. (pl. 74, fig. 27); 2.0, 3.6, 1.5, 1.6 mm.; 2.2, 4.0, 1.4, 1.6 mm. (pl. 74, fig. 29).

The length and width of five hypostomas are, respectively, 0.8, 0.9 mm. (pl. 74, fig. 17); 0.9, 1.1 mm.; 1.1, 1.4 mm.; 1.1, 1.3 mm.; 1.9, 2.4 mm.

The length and width of seven pygidia are respectively, 0.4, 1.2 mm. (pl. 74, fig. 15); 0.5, 0.7 mm. (pl. 74, fig. 12); 0.6, 1.2 mm.; 1.0, 2.4 mm.; 1.0, 2.2 mm.; 1.2, 2.7 mm.; 1.3, 3.2 mm.

Family TRINUCLEIDAE Emmrich, 1845
Subfamily CRYPTOLITHINAE Bancroft emend. Whittington, 1941
Genus CRYPTOLITHUS Green, 1832
CRYPTOLITHUS TESSELATUS Green, 1832
Plate 75, figures 1–26, 46

The present material adds a little information to that given in my recent description of this species (1941, p. 29).

A count of the pits in the fringe on each side of E_1 in fifty specimens shows that nearly 80 per cent have between 19 and 22 pits, the remainder having one or two additional pits. I_3 commences at the fourth to seventh (80 per cent at the fifth to sixth) pit of I_2 from the axial furrows. In only two specimens I_3 reached forward to the axial furrow. Within this fairly narrow range of numbers of pits in the fringe, the arrangement is very constant, in concentric rows, I_1 a little depressed, a very strong concentric ridge between I_1 and I_2, and radial ridges between pits anterior to the glabella. The raised radial plates in E_1 show every variation between being indistinguishable and very conspicuous.

Størmer (1930, pp. 102–103) has discussed the structure of the pits in the fringe of *Tretaspis*. The pits of *C. tesselatus* are similarly constructed. The pits in each lamella always correspond, and their flattened bases, separated by the marginal suture, are in juxtaposition. In the center of the base is a small circular area which seems to be an opening connecting the pits.

The inner edge of the lower lamella of the fringe is thickened anteriorly and continued laterally as a concentric ridge within I_2.

On the inner surface of the cephalon the pair of short glabellar furrows are the location of short, stout appendifers. The lateral pits of the occipital furrow are similarly extended ventrally. The occipital ring is thickened at the posterior border and drawn out into the stout, hollow spine. There is no posterior doublure. The marginal extremities bear, on the ventral surface, the rounded articulating processes,[1] on each side of each of which are shallow articulating sockets. As seen in ventral aspect, there is a faint,

[1] These processes have been noted as "pits" in casts of *Onnia ornatus* (Whittington, 1940, p. 253).

broad, shallow furrow crossing the glabella a short distance anterior to the ridge representing the occipital furrow. This furrow is very inconspicuous on the dorsal surface as a corresponding ridge (see pl. 75, fig. 46).

The anterior pits appear on the inner surface as small rounded processes, the anterolateral slope being steep.

The posterior margin of the cheek lobes is thickened, but lacks the doublure. On the inner part of the posterior margin of the upper lamella of the fringe there is a narrow doublure separated from the lower lamella by the marginal suture, which is thus ventral for this very short distance.

The first segment of the thorax differs from the others and from the pygidium in not possessing the articulating half ring. Thus on enrollment a lenticular space opens between the occipital ring and the axial ring of the first segment, which is protected dorsally by the occipital spine. On the inner surface the articulating furrow carries laterally the short, stout appendifers. The transversely striated doublure is present on the axial ring of all the segments. The axial furrows at the anterior margin are excavated into the articulating sockets, on each side of which are small articulating processes. On the posterior margin are the rounded, ventrally directed, articulating processes, flanked by the small sockets, exactly as on the margin of the occipital ring. The large sockets on the anterior margin slope ventrally and posteriorly, and thus on enrollment receive the ventrally directed processes on the posterior margin. The pleurae of the first segment differ from those of succeeding segments in that the anterolateral extremities are cut off diagonally, and therefore fit closely against the cephalic margin. The pleurae of the succeeding segments are flexed backwards laterally and turned down at their extremities (see pl. 75, figs. 21, 22, 24–26).

On the inner surface of the pygidium only the first axial ring has a pair of short appendifers. The anterior margin has the large articulating sockets and small articulating processes at the axial furrows. Two paired rows of dark spots, possibly areas of muscle attachment (cf. Størmer, 1930, pp. 93–94), are seen on the rachis. The outer rows are largest, elongated transversely, and appear to be correspondingly situated to the appendifers of the first segment. The inner rows are much smaller, subcircular in outline, and become separate from the outer rows only at about the fourth segment, apparently by shortening of the size of the outer spots (pl. 75, fig. 20), which extend less and less farther axially posteriorly. The posterolateral margin of the pygidium is bent down, but there is no doublure. In posterior view the wide margin is notched axially.

Development.—The development of *Cryptolithus tesselatus* is very similar indeed to that of *Onnia ornatus* and other species of *Cryptolithus* (see Whittington 1940, 1941). One complete enrolled specimen (pl. 75, fig. 5) shows that the smallest cephala in the material belong to degree 0, i.e., there are no thoracic segments. The glabella is carinate, with steep, flat sides and a prominent median tubercule. The alae are large, not crossed by the occipital furrow. The occipital ring is very gently convex, without the axial spine. The cheek lobes show the coarse reticulate ornament. The lateral eye tubercles, situated a little farther forward than the anterior end of the alae, are large, with strong lists crossing the axial furrows. The fringe is narrow, having the appearance of a rolled margin to the cephalon and forming a continuous structure with the long, curved genal spines. The marginal suture is on the dorsal surface, at the anterior edge, and posterolaterally curves around and across the posterior cephalic margin to become ventral for a short distance. The upper lamella is thus very narrow, the lower considerably wider and curled over dorsally at the outer edge. One concentric row of pits, about 20 on each side, on the inner margin. No additional pits posterolaterally. The inner edge of the lower lamella is thickened anteriorly. The short doublure of the posterior margin of the fringe is present. The genal angles are not in advance of the posterior margin of the rest of the cephalon.

A complete enrolled specimen at degree 2 (pl. 75, fig. 4) has the glabella still strongly carinate. The alae are considerably narrower, the first glabellar furrows and the lateral pits of the occipital furrow faintly developed in the furrows separating the glabella, the alae and the occipital ring. The latter is a little more convex, without the

spine. On the inner surface the two pairs of appendifers are faintly developed, as also are the anterior pits in the axial furrows immediately anterior to the eye lists. The large lateral eye tubercles are closer to the glabella, the lists consequently shorter. The glabella and the cheek lobes are coarsely reticulated.

The fringe has three complete concentric rows of pits, one or two additional pits posterolaterally. The concentric ridge on the upper lamella between I_1 and I_2 is present anterolaterally and laterally. Externally to E_1 the rolled margin of the fringe is relatively broad, the marginal suture on the dorsal surface. The lower lamella is flat, not V-shaped in cross section anteriorly, the girder weak. The inner edge is thickened and forms a smooth curve.

With increasing size the convexity of the cephalon is greater. The glabella is less strongly carinate and becomes clavate. The occipital ring increases in convexity, the alae are reduced in length and width, and on the inner surface the appendifers of the glabella and occipital furrows and the articulating processes and sockets are more strongly developed. Concomitantly the anterior pits gradually deepen. The occipital spine appears and gradually increases in length. The lateral eyes and eye lists are reduced and disappear. The reticulate ornamentation on the glabella and cheek lobes is retained but appears relatively less coarse.

The margin of the fringe, instead of being a curved surface connecting the lamellae, becomes flattened and slopes steeply downwards, most steeply anteriorly, and makes an obtuse angle with the upper lamella and an acute with the lower. The suture is very close to the dorsal edge, and thus in the adult the edge of the upper lamella is sharp, that of the lower lamella flexed back dorsally to form the narrow margin. The additional pits posterolaterally increase in number, and I_3 gradually extends farther forwards. At a slightly larger degree than 2, the inner edge of the lower lamella is indented anteriorly beneath the glabella (pl. 75, fig. 15). With increasing size this indentation becomes more pronounced, the girder deepens very considerably, and the lower lamella becomes anteriorly V-shaped in cross section, pits 3 and 4 of I_1 and I_2 being fused together in front of the glabella (see pl. 75, figs. 15, 13, 18). The genal angles become prolonged beyond the rest of the cephalon.

The smallest transitory pygidium is subsemicircular in outline (pl. 75, fig. 5). The rachis is most strongly convex posteriorly, and behind the first axial ring forms with the inner parts of the pleural lobes a convex area. The lateral parts of the pleural lobes are flat. The margin posterior to the rachis is notched. On the inner surface the appendifers of the first two or three segments are faintly developed. With increasing size the pleural lobes flatten, the central convex area is consequently reduced in size, and the rachis becomes more distinct. There is a change in outline of the pygidium, from subsemicircular to subtriangular, most probably at about the same time as the change from the transitory to the true pygidium. In the true pygidium only the appendifers of the first segment are strongly developed.

Dimensions.—The sagittal length and maximum width of several individuals of *Cryptolithus tessalatus* are as follows. The length and width of the cephalon and the length and width of the glabella of 32 specimens are, respectively, 0.5, 1.4, 0.4, 0.3 mm.; 0.6, 1.4, 0.4, 0.3 mm. (pl. 75, fig. 1); 0.6, 1.3, 0.4, 0.3 mm. (pl. 75, fig. 5); 0.7, 2.0, 0.6, 0.5 mm.; 0.8, 2.0, 0.5, 0.4 mm. (pl. 75, fig. 3); 0.9, 2.6, 0.7, 0.6 mm.; 1.0, 2.7, 0.7, 0.5 (pl. 75, fig. 4); 1.0, 2.5, 0.7, 0.5 mm.; 1.5, 3.5, 1.0, 0.7 mm.; 1.8, 4.0, 1.4, 1.0 mm.; 1.8, 4.0, 1.1, 0.7 mm. (pl. 75, fig. 11); 1.9, 4.5, 1.3, 1.0 mm. (pl. 75, fig. 12); 1.9, 4.2, 1.5, 1.0 mm.; 2.1, 4.3, 1.2, 0.9 mm.; 2.2, 4.3, 1.3, 0.9 mm.; 2.3, 4.8, 1.5, 1.1 mm.; 2.4, 4.8, 1.5, 1.1 mm.; 2.5, 5.7, 1.8, 1.4 mm.; 2.6, 5.1, 1.8, 1.3 mm.; 3.0, 6.2, 2.2, 1.7 mm.; 3.1, 6.5, 2.1, 1.4 mm.; 3.1, 6.2, 2.1, 1.6 mm.; 4.0, 8.1, 3.0, 2.0 mm.; 4.1, 8.9, 3.9, 2.2 mm.; 4.2, 8.4, 3.0, 1.9 mm.; 4.2, 8.6, 2.5, 2.5 mm.; 4.3, 7.5, 2.5, 1.8 mm.; 4.5, 9.4, 3.4, 2.6 mm.; 4.5, 8.6, 3.1, 2.1 mm.; 6.4, 11.4, 4.7, 3.4 mm.; 7.7, 14.9, 6.0, 4.8 mm.; 8.2, 15.5, 6.5, 4.7 mm.

The length and width of 14 pygidia are, respectively, 0.4, 1.5 mm.; 0.5, 1.4 mm.; 0.5, 1.7 mm.; 0.5, 1.7 mm.; 0.8, 2.7 mm.; 0.8, 2.7 mm.; 0.8, 2.4 mm.; 1.2, 3.5 mm.; 2.6, 7.0 mm.; 2.8, 7.1 mm.; 2.8, 7.6 mm.; 3.2, 7.8 mm.; 3.3, 8.6 mm.; 3.6, 9.3 mm.

Family OTARIONIDAE R. and E. Richter, 1926

Genus OTARION Zenker, 1833

OTARION sp.

Plate 72, figures 28–30, 35–37, 41

A few cranidia and isolated free cheeks that belong to a species of *Otarion* are present in the material.

The convex glabella narrows and is rounded anteriorly, and stands high above the rest of the cephalon. The basal lateral lobes are suboval in outline, elongated longitudinally, very convex, and reach forward to a point opposite the middle of the palpebral lobes. The glabellar furrows delimiting them are deep and run obliquely backwards into the occipital furrow. Occipital ring strongly convex, with a median tubercle, the posterior margin arched backwards, the doublure lenticular in outline and reaching forward nearly to the occipital furrow. The latter is shallow and broad medially, deep and narrow behind the glabellar lobes. Axial and preglabellar furrows moderately deep, and forming a smooth curve around the anterior end of the glabella; anterior pits absent. The axial furrows deepen as they swing around and in behind the lateral lobes.

The preglabellar field wide, convex transversely, with a broad, rolled margin. The palpebral lobes, situated opposite a point about two-thirds the length of the glabella, are the highest point of the fixed cheeks. Posterior marginal furrow moderately deep, posterior margin convex, the doublure narrow near the axial furrows and widening laterally.

The free cheeks subtriangular in outline, sloping steeply down in a concave curve to the wide, rolled border, which is prolonged posterolaterally into the genal spine. The doublure is narrow, and bent up under the border. The anterior branches of the facial sutures diverge slightly forward across the cheeks, then curve and run along the vertical margin of the preglabellar field towards the median line before cutting the doublure. Thus the doublure of the free cheeks is extended anteromedially under the preglabellar field. There are not sufficient well-preserved specimens to show whether the anterior branches of the facial sutures unite to form a median suture crossing the doublure, or whether they cross it parallel and close together as connective sutures.

Except in the furrows and on the borders the cephalon is ornamented with well-spaced, rounded tubercles, the intervening areas being apparently smooth.

The smallest cranidia have the glabella only slightly wider posteriorly than anteriorly, and the lateral lobes are small and faintly outlined. The axial and preglabellar furrows are very shallow. The preglabellar field is relatively longer than the adult. The eyes are proportionately large and a little farther laterally from the axial furrows than in the adult.

Slightly larger cephala show that the axial and preglabellar furrows deepen, the lateral lobes become well-defined, larger, and more strongly convex. Concomitantly the fixed cheeks slope more steeply inwards to the axial furrows.

Family ASAPHIDAE Burmeister, 1843

Subfamily ASAPHINAE Raymond, 1910

Genus ISOTELUS Dekay, 1824

ISOTELUS sp.

Plate 75, figures 27–45, 47

Among the specimens from the Spring Hill locality are a few cranidia, isolated free cheeks, hypostoma and pygidia which may be referred to *Isotelus* sp. Most of the specimens are small and probably belong to the early holaspid degrees. There are also a few fragments of larger individuals.

The ontogeny of *Isotelus gigas* Dekay has been discussed by Raymond and Narraway (1910, pp. 53–56) and by Raymond (1914). The present material agrees very closely with this species and probably belongs either to it or to *I. iowensis*.

The small cephala have the glabella outlined by the shallow axial and preglabellar furrows. The occipital furrow is faintly developed laterally, and a pair of glabellar furrows, directed obliquely backwards, are situated opposite the palpebral lobes. These furrows show very faintly on the inner surface of the cephalon. The doublure of the occipital ring is narrow.

The striated doublure of the free cheeks is flat anteriorly, united by the median suture. Anterolaterally and laterally it is flat marginally and flexed dorsally inwards so

that the edge lies close to the under side of the dorsal surface. At the posterolateral corner the doublure is pierced by a small circular hole, and a short distance anteriorly to this hole some of the specimens show a short wrinkle in the curved surface (see pl. 75, fig. 47). The circular hole is the Panderian organ (see Raymond, 1920, pp. 90–91). The organ is also visible on the doublure of the thoracic segments, situated nearest to the anterior edge and well within the termination (see pl. 75, fig. 44; cf. Raymond, 1920, fig. 28, p. 91). In ventral aspect the anterior edge of the suboval opening is raised, and thus the orifice is directed posteriorly. This structure agrees with that of *Asaphus expansus* illustrated by Volborth (1863, pl. 1, fig. 1).

The smallest pygidia are subsemicircular in outline, the margin posteriorly to the rachis notched. The segments are most clearly demarcated anteriorly, with shallow pleural furrows. With increasing size the segments become unmarked forwards, and the pygidium becomes smooth, with only the shallow axial furrows. The striated doublure is wide and flexed dorsally to lie close to the dorsal test. The inner edge is notched beneath the rachis.

The hypostoma is known from a few large fragmentary specimens. The outline is subquadrangular, the posterior border deeply forked. There are no anterior lateral or posterior furrows. The anterolateral margins are bent dorsally and extended as the anterior wings, the much smaller posterior wings being formed by an extension of the margin on the dorsal side at the base of the fork. A pair of suboval maculae are situated opposite the posterior edge of the anterior wings. The stout forks of the posterior border are bluntly pointed, triangular in cross section, the ventral surface being flat. The hypostoma is ornamented by widely spaced, anastomosing lines running in a longitudinal direction. These lines are absent or inconspicuous in the median area and do not cross the maculae but swing around them. A different ornamentation is seen only on the sloping inner surface of the fork, where the lines are very close and do not anastomose (pl. 75, fig. 41).

Two fragments of the thoracic segments show the presence of articulating joints in the axial furrows. A horizontally elongated socket and process is present on the anterior and on the posterior edge, the anterior edge having the process on the inner side, the posterior edge on the outer (pl. 75, fig. 45). The inner surface of the axial ring is smooth, without the articulating furrow and appendifers, and with a narrow posterior doublure.

III. DISCUSSION

The eye and the segmentation of the cephalon.—Öpik (1937, pp. 126–134) has summarized the arguments for believing that the eye and the eye ridges of the trilobite belong to the fifth segment of the cephalon.

The axial ring of each segment of the thorax and pygidium of *Diacanthaspis cooperi* bears a pair of prominent spines, as does the occipital ring of the cephalon. The glabella of the second largest cephalon of the developmental stages bears four pairs of similar spines, which have been termed the axial spines. A further pair occur on the preglabellar field. It may be that these six prominent pairs of spines on the young cranidium represent the number of segments in the cephalon. This is supported by the fact that the two most posterior pairs on the glabella are opposite the two pairs of glabellar lobes and occur opposite the posterior part of these lobes in a position corresponding to the pair on the occipital ring. In the smallest cranidium the second pair are not developed, but the first glabellar furrows are present. The eye ridges occur opposite the fifth axial spines, i.e., are presumably thus connected with the fifth cephalic segment. It is considered by Öpik and other authors that there are, at least in some trilobites, two segments on the dorsal side of the cephalon anterior to the fifth segment. The sixth segment may be represented by the pair of spines which appear in the second smallest cranidium between the fifth and sixth axial spines, the preglabellar field with its furrow thus representing the seventh segment.

Assuming that the rachis of the protaspis of *Flexicalymene senaria* is divided as suggested above, then there are four short segments, a larger anterior segment, and the narrow preglabellar field representing the axial region of the cephalon (see pl. 72, fig. 1). The eye ridges are opposite the larger

anterior segment of the glabella, which may in reality represent two fused segments. Thus the eye ridges are again associated with the fifth segment of the cephalon, and the dorsal surface is probably made up of seven fused segments. The anterior position of the eye, immediately posterolateral to the lateral extremities of the preglabellar field, strongly suggests that the free cheeks, and thus the visual surface of the eyes, are the pleural parts of the preglabellar, or seventh, segment.

The fifth segment of the cephalon bears the antennae, according to Jaekel (1901). Öpik regards the loss or reduction of the appendifers of this segment in many trilobites as indicating that the antennae are no longer attached to the under side of the test as such, but have been modified to become the eyes on the cheeks (1937, p. 132). These eyes he regards as one stage in the evolution of the antennae and their nervous system in the trilobite (1937, p. 133).

In a previous publication (1929) Öpik has put forward the view that in *Pseudasaphus* the hypostoma and free cheeks are bound together in a unit, to which unit only slight movement is possible. After feeding, the contraction of the stomach muscles would set up a vibratory movement in this unit (p. 15). The visual surface of the eye is attached to the free cheeks and would thus also take part in the movement. He further suggests that the type of eye with many lenses would maintain a more or less continuous field of view during this movement (p. 16). The structure of the free cheeks, epistoma and hypostoma of *Ceraurus*, *Flexicalymene*, and *Isotelus* is described below. If in these three genera a movement of the hypostoma necessitated complementary movements of the epistoma and free cheeks, then the suggestions made by Öpik in regard to *Pseudasaphus* might be valid for them also.

In *Cryptolithus* the eye ridges are lost early in the development, and thus presumably the nerve system of the antennae. The fringe may be a specialized development serving as a sensory organ in place of the antennae (or eyes). The related genus *Tretaspis*, however, has the lateral eyes present in the adult, and they consist of a single lens (Størmer, 1930, pp. 89–91).

The attachment of the hypostoma.—The hypostoma of *Ceraurus pleurexanthemus* is united by the hypostomal suture to the epistoma and the anterior doublure of the free cheeks. It would seem, from the size and weight of the hypostoma, mechanically necessary to have some further connection with the rest of the cephalon. The structure of the dorsal extremities of the anterior wings of the hypostoma and the inner surface of the anterior pits of the axial furrows strongly suggests a connection between these points. The bosses on the anterior wings would fit into the circular pits on the inner anterior surface of the anterior pits. The flange formed by the edge of the anterior wings immediately behind the bosses would thus be in contact with the posterior slope of the inner surface of the anterior pit

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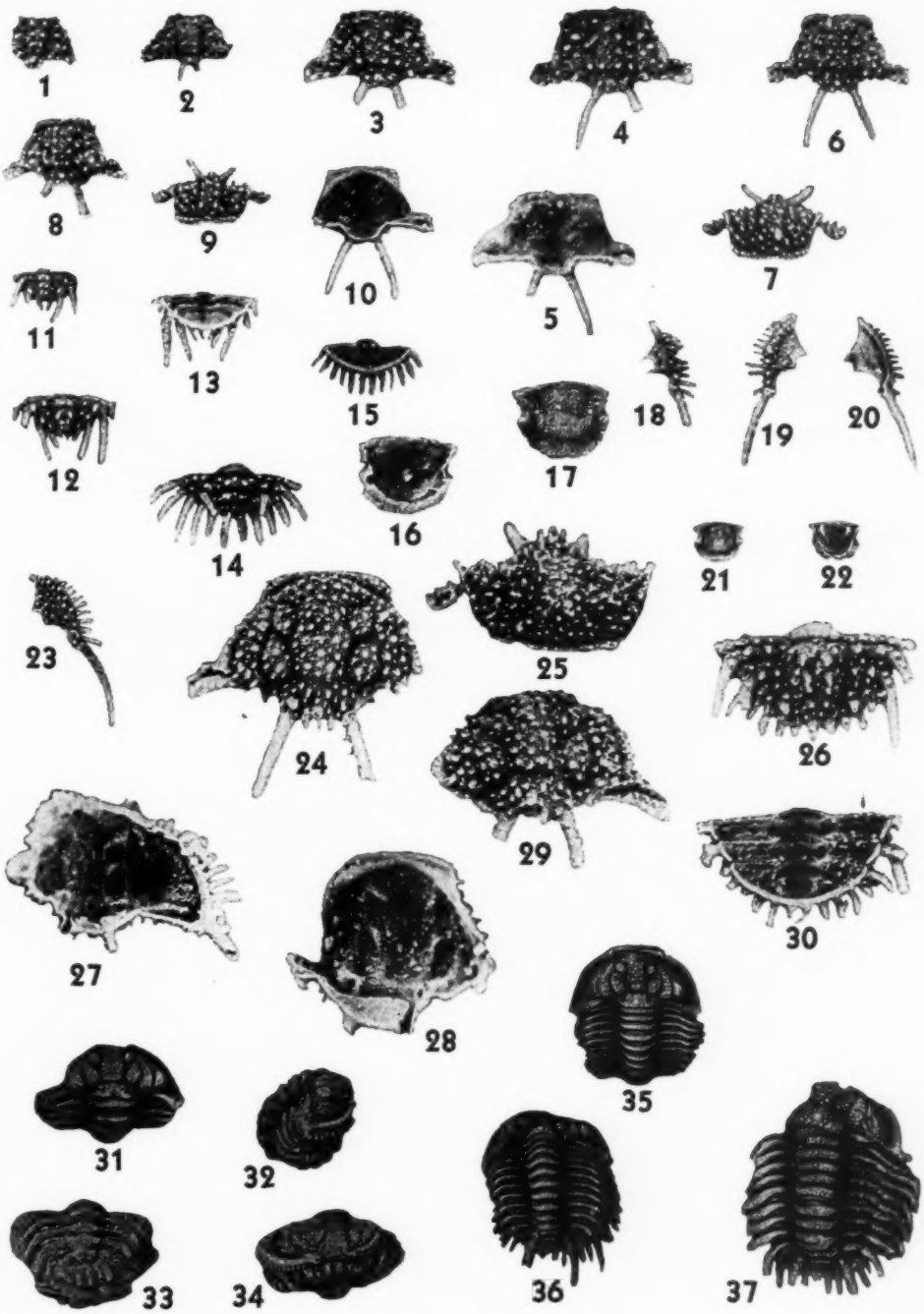
EXPLANATION OF PLATE 74

FIGS. *1–30*—*Diacanthapsis cooperi* Whittington, n. gen., n. sp., untouched photographs. All are in the United States National Museum from 2½ miles NNE. of Spring Hill, Va., *1*, Incomplete cranidium, dorsal view, ×15. *2*, Cranidium, dorsal view, ×15. *3*, Dorsal view, ×15. *4*, *5*, Dorsal and ventral views, ×15. *6*, *7*, *10*, Cranidium, dorsal, anterior and ventral views, ×10. *8*, *9*, Dorsal and anterior views, ×10. *11*, Transitory pygidium, dorsal view, ×15. *12*, *13*, Transitory pygidium, dorsal and ventral views, ×15. *14*, Syntype, pygidium, dorsal view, ×10. *15*, Pygidium, ventral view, ×10. *16*, *17*, Hypostoma, dorsal and ventral views, ×15. *18*, Free cheek, dorsal view, ×10. *19*, *20*, Free cheek, dorsal and ventral views, ×10. *21*, *22*, Hypostoma, ventral and dorsal views, ×5. *23*, Syntype, free cheek, dorsal view, ×5. *24*, Cranidium, anterodorsal view, ×10. *25*, *29*, Syntype, cranidium, anterior and posterolateral views, ×10. *26*, *30*, Syntype, pygidium and two thoracic segments, dorsal and ventral views, ×10. *27*, Syntype, incomplete cephalon, ventral view, ×10. *28*, Cranidium, ventral view, ×10. (p. 502)

FIGS. *31–37*—*Leonaspis? trentonensis* (Hall), untouched photographs. *31–34*, Holotype, almost complete enrolled individual, dorsal, lateral, posterior, anterior views; Trenton, Bay of Quinta, Ontario, Canada. American Museum of Natural History, type no. 853/2, ×3. *35*, *36*, Complete individual, dorsal views; Trenton, Trenton Falls, New York State Museum, ×3. *37*, Almost complete individual, dorsal view; Trenton, Trenton Falls, New York State Museum, ×3. (p. 502)



Whittington, Trenton Trilobites

Whittington, Trenton Trilobites

(text figs. 7, 8). It may be assumed that the anterior wings and the anterior pits functioned together in a manner similar, say, to the articulating joints of the thorax. It seems likely that the hypostoma moved about these two joints, since if no movement took place, probably they would have fused together in a fixed position. The hypostoma is thus braced firmly against the cephalon at two joints, and movement is limited to a rocking motion about these joints in a vertical plane. Upward movement of the posterior end would be limited, however, by the flanges behind the bosses on the anterior wings. The converse movement, i.e., downward at the posterior end, depends entirely on the nature of the union across the hypostomal suture. If a membrane were present, a considerable movement might be possible. If not, then it would seem that the free cheeks, epistoma, and hypostoma were bound together in a unit, and the outline indicates that they can fit together very closely (cf. *C. aculeatus*, Öpik, 1937, pl. 17, figs. 2, 3). It would seem to follow in this case that the movement at any suture would necessitate complementary movements at the other sutures.

This structure of the cephalon, in which very slight movements only are possible for a very strongly anchored hypostoma, accords very well with Öpik's interpretation of the structure of the cephalon of *Pseudasaphus tecticaudatus* (1929, pp. 12–16, etc.). In this case the hypostoma is attached to the doublure of the free cheeks by the hypostomal suture, the anterior wings, probably part of the posterior wings, and the indented margin between the wings. The hypostoma and the free cheeks thus form a unit, attached by the facial sutures to the glabella and fixed cheeks. Öpik suggests that muscle contraction after feeding would cause a vibratory movement of the hypostoma, which would be shared by the free cheeks, and the elasticity of the glabella and fixed cheeks would enable them to yield also. He further suggests that the currents of water moving over the test during swimming would initiate similar movements.

Stubblefield (1936, p. 410) has expressed doubt as to whether movement at the epistomal or hypostomal suture of the trilobite would necessitate complementary movements at the remaining sutures. However, it seems that such complementary movements of *Ceraurus* would occur if there were not a membrane at the hypostomal suture. Movements of the free cheeks, on the other hand, would presumably occur about the eye as a fulcrum, and the outline along the sutures, particularly at the connective sutures and the posterolateral parts of the

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EXPLANATION OF PLATE 75

Untouched photographs of specimens all except *21*, *22*, *25*, and *26* from 2½ miles NNE. of Spring Hill, Va., in the United States National Museum.

FIGS. *1–26*, *46*—*Cryptolithus tesselatus* Green. *1*, *2*, *6*, Cephalon, dorsal, anterior and ventral views, ×15. *5*, The enrolled meraspid trilobite, degree 0, ventral view, ×15. *3*, *7*, Meraspid cephalon, ventral and dorsal views, ×10. *4*, The enrolled meraspid trilobite, degree 2, ventral view, ×5. *8*, *9*, The cephalon, at probably meraspid degree 2, dorsal and anterior views, ×5. *10*, Transitory pygidium, dorsal view, ×10. *11*, *15*, Cephalon, dorsal and ventral views, ×5. *12*, *13*, *16*, Cephalon, dorsal, ventral and anterior views, ×5, ×3, ×5. *14*, Transitory pygidium, ventral view, ×10. *17*, *18*, Lower lamella of fringe, dorsal and ventral views, ×1, ×2. *19*, Cephalon, anterior view, ×1. *20*, Pygidium, ventral view, ×2. *21*, *22*, Anterior thoracic segment, dorsal, and ventral views, 3 miles NNE. of Long Glade, Va., ×2. *25*, *26*, Segment of thorax, not the anterior, dorsal and ventral views, 3 miles NNE. of Long Glade, Va., ×2. *24*, Thorax, ventral view, ×5. *23*, Incomplete enrolled holaspid, posteroventral view, ×2. *46*, Cephalon, anterior view of ventral surface, ×3. (p. 509)

FIGS. *27–45*, *47*—*Isotelus* sp. *27*, Cranidium, dorsal view, ×5. *28*, *29*, Cranidium, dorsal and ventral views, ×3. *30*, *31*, Hypostoma, ventral and dorsal views, ×5. *32*, *33*, Hypostoma, ventral and dorsal views, ×1. *41*, Hypostoma, lateral view of dorsal surface, ×5. *34*, *35*, Pygidium, dorsal and ventral views, ×5. *36*, Pygidium, dorsal view, ×5. *39*, Pygidium, dorsal view, ×3. *37*, *38*, Pygidium, dorsal and ventral views, ×3. *42*, *43*, Pygidium, dorsal and ventral views, ×2. *44*, Extremity of thoracic segment, ventral view, showing the Panderian organ, ×2. *45*, Part of thoracic segment, ventral view, ×1. *40*, Free cheek with visual surface of eye attached, dorsal view, ×2. *47*, Free cheek, ventral view, showing Panderian organ and wrinkle in doublure, ×2. (p. 512)

doublure, seems to be expressly designed for stability.

The attachment of the hypostoma, therefore, is such that it is braced firmly in a fixed position relative to the rest of the cephalon, and some movement is possible in the vertical plane. If there is a membrane at the hypostomal suture, then the possible movement may be quite considerable, if not, then the possible movement is very slight, perhaps of a vibratory type as suggested by Öpik for *Pseudasaphus*.

Stubblefield (1936, pp. 410–414, etc.) has discussed the views of the proponents of the two theories of the origin of the epistomal (rostral) suture, that it is either a relic of a former longer suture or a subsequent development. If it be true that the hypostoma, epistoma, and free cheeks moved in a unit in certain trilobites, then the epistomal suture may have facilitated this movement and have been in part retained or developed for this purpose.

The hypostoma of *Flexicalymene senaria* is united by the hypostomal suture to the epistoma and the inner anterior corners of the doublure of the free cheeks. In addition, there is a stout boss on the inner surface of the anterior wings of the hypostoma, which appears to articulate with the socket in the anterior slope of the inner surface of the anterior pits (cf. Raymond, 1920, p. 55). The anterior wings (side lappets) show pits on the outer, lower surface, not as Raymond states, on the inner, upper surface. Behind the boss the edge of the anterior wing is extended as a flange, which would rest against the posterior slope of the inner surface of the anterior pits (see text figs. 9, 10). This attachment of the hypostoma of *Flexicalymene* is very similar indeed to that of *Ceraurus*. The arguments and suggestions offered in the discussion above in relation to the hypostoma of *Ceraurus* can thus be applied, in the main, equally well to *Flexicalymene*.

An unusual feature of the hypostoma of *Flexicalymene* is that the anterior border is flexed sharply ventrally. This means that the anterior end of the hypostoma is well above, i.e., a short distance dorsally from, the rolled anterior border of the cephalon, which is made up of the doublure of the free cheeks, the preglabellar field, and the epistoma. Thus, on enrollment, when the rolled posterior border of the pygidium is tucked inside the anterior border of the cephalon, the hypostoma is well inside and does not interfere with the most efficient enrollment for protection.

Comparatively little information can be gleaned as to the manner of attachment of the hypostoma of *Diacanthaspis*. The epistomal suture is marginal, and the epistoma appears to be a very short curved plate. The hypostoma was united at the curved anterior edge to the epistoma and perhaps to the anterior edge of the doublure of the free cheeks. No definite anterior pits can be distinguished, unless the increased deepening of the preglabellar furrow on the fixed cheeks anterolaterally to the eye ridges can be so regarded. On the inner surface there is no sign of an articulating socket, and no corresponding boss is seen on the anterior wings of the hypostoma. Thus it is possible that the attachment of the hypostoma of *Diacanthaspis* was only by the hypostomal suture and by muscles, although the small size of the species and the coarseness of the silicification prevents any certainty on this point.

In his discussion of *Pseudasaphus tecticaudatus*, Öpik described two lunate muscle areas on the glabella, which extend forward from between the anterior end of the eyes (1929, pp. 4–10, text figs. 1–4). He points out that these muscle areas are situated vertically over the middle body of the hypostoma. He considers the ventral side of the forked posterior border, the maculae, and perhaps the anterior border, to be areas of attachment of the hypostoma (1929, pp. 10–11). The test of *Ceraurus pleurexanthemus* appears to show no such comparable muscle attachment fields. The largest tubercles on the glabella have been described as occurring within a suboval area extending from in front of the occipital furrow to just anterior to the third glabellar furrows. This general area lies vertically above the middle body of the hypostoma, but it seems perhaps unlikely that these tubercles are connected with areas of muscle attachment, since apparently similar tubercles occur on the frontal slope of the glabella and on the fixed cheeks and much more numerously on the cephala of other species (e.g. *C. aculea-*

tus). The hypostoma of *C. pleurexanthemus* is without maculae (in contrast to *C. aculeatus*—Öpik, 1937, pl. 17, fig. 4). The posterior wings suggest themselves as areas of attachment.

There are no features on the median area of the glabellae of *Flexicalymene senaria* or *Diacanthaspis cooperi* that are suggestive of points of areas of muscle attachment. On the hypostomae, the deepenings in the lateral furrows, the middle furrow, and the posterior wings may be points of muscle attachment.

In the genus *Reraspis* (Öpik, 1937, text fig. 29, p. 109) the anterior pits are not situated at the anterior end of the axial furrows and are, in contrast to *Flexicalymene* and *Ceraurus*, posterior to the intersection of the eye ridges and the axial furrows. In addition to this apparent difference in position in different genera, the function of these pits may not be the same in all trilobites in which they occur. Raymond (1920, p. 63, fig. 20) has presented a restoration of the under surface of *Cryptolithus tesselatus* in which the antennules are attached to the anterior pits, and the hypostoma to the inner edge of the lower lamella of the fringe (see also p. 62, p. 159, fig. 45, pl. 7, fig. 1). This position of attachment of the hypostoma is clearly not possible, if, as suggested below, in enrollment the posterior margin of the pygidium fits against the inner edge of the lower lamella. It is possible that a flat hypostoma with a straight anterior edge was attached to the anterior pits, but the latter are smooth on the inner surface and offer no evidence on this point; such a hypostoma would be very different from that of the specimen on which Raymond's restoration is based. It is very remarkable, having regard to the fact that *C. tesselatus* is the most abundant trilobite in the material studied, that no trace of the hypostoma of this species has been found. The entire shell of *C. tesselatus* and of the other species, including their hypostoma, has been silicified. It may be, therefore, that the hypostoma was not constructed of the same material as the rest of the shell of *C. tesselatus*, and was therefore weakly or not at all silicified.

To summarize: evidence has been reviewed that suggests, in my opinion, that the hypostoma of *Ceraurus* and *Flexicalymene* was attached to the cephalon by the hypostomal suture and a pair of articulating joints between the anterior wings and the anterior pits. It is not inferred, however, that the anterior pits functioned as a support to the hypostoma in all trilobites. Their position is somewhat variable, their function in *Cryptolithus* not certainly known, and they are absent in many trilobites with hypostoma. The attachment of the hypostoma in three widely differing genera, *Pseudasaphus*, *Ceraurus*, and *Flexicalymene*, is such that the hypostoma is firmly fixed relative to the rest of the cephalon, movement being possible in one plane only, the actual amount of movement uncertain. The suggestion is offered, from negative evidence, that the hypostoma of *Cryptolithus* may not have had the same shell structure as the dorsal test.

The appendifers.—The appendifers have been discussed by Öpik (1937, pp. 8–11) and by Størmer (1939, pp. 166–167). They occur on the axial ring of the thorax and pygidium at the lateral extremities of the articulating furrow, i.e., at the anterior margin of the segment. They are not always "processes extending downwards from the dorsal test" (Raymond, 1920, p. 20), as Öpik has recognized (p. 9). This is very clearly seen in the case of *Flexicalymene senaria*. In this species the articulating furrow is broad and shallow axially, slightly narrower and with steeper sides laterally, changing from a U- to a V-shaped cross section. In *Diacanthaspis cooperi* the articulating furrow remains broad and shallow in cross section laterally, and appendifers as such seem to be absent. In *Isotelus* sp. the articulating furrow is not present. This feeble development or absence of appendifers contrasts strongly with the condition in *Cryptolithus* and *Ceraurus*.

Appendifers are developed in the occipital and glabellar furrows of *Ceraurus* and *Cryptolithus*, but feebly or not at all in those of *Flexicalymene*, *Diacanthaspis* and *Isotelus*. The reason for this striking difference in the development of the appendifers is not apparent.

Öpik (1937, e.g. text fig. 36, p. 124) has followed Jaekel (1901) and regards the anterior pits as belonging to the preglabellar furrow and as the homologues of the appendifers of the glabellar furrows, and the

seat of attachment of the antennulae (1937, p. 102). I have here interpreted the anterior pits[1] of *Ceraurus* and *Flexicalymene* as the sockets of articulating joints with the hypostoma, and this is in accord with the observations of Barrande (1862, p. 230) on *Cheirurus*, and Raymond on *Calymene* (1920, p. 55). It would seem that the antennulae would not need such a strong attachment as the anterior pits afford, and on these grounds alone I would regard them as being more likely to be associated with the hypostoma. It is at least arguable that the anterior pits in these two genera are homologous with the appendifers of the occipital and glabellar furrows. They are situated at the intersection of the preglabellar and axial furrows, not within the preglabellar furrow as the appendifers are within the occipital and glabellar furrows, and their function, as I interpret it, is rather different. They may be regarded as appendifers modified to a special function, but equally well as a special structure developed to support the hypostoma, and developed, it may be noted, at the point where the test is especially rigid. It seems probable that in *Cryptolithus* the anterior pits did not serve as supports to the hypostoma, and their function is doubtful.

The appendifers in the genera studied are thus developed to very different degrees. In any one genus they are developed in the segments of the cephalon posterior to the fifth (or eye) segment (the postoral appendifers), the thorax, and the anterior pygidial segments. The fifth cephalic segment has been greatly modified, losing its appendifers (see above), and it seems that, in some genera, the sixth (or antennular) segment has also been greatly modified, and has developed special processes (or modified the appendifers), to support the hypostoma. Thus the anterior pits of such genera may not be the homologues of the postoral appendifers. In other genera the function of the anterior pits is uncertain; they may have been points of attachment for the antennulae.

[1] For summary of, and references to, views on the function of these pits, see Whittington, 1941. See also King, 1914, pp. 393–394; Woodward, 1884, pp. 71–76; Størmer, 1930, pp. 94–95.

The development.—In the early stages of the development of *Flexicalymene* and *Diacanthaspis* the abundant spines on the cephalon and pygidium are notable. As *Flexicalymene* increases in size the cephalic spines are reduced to become tubercles, including the genal spines. The spines on the margin of the pygidium are reduced and disappear. In *Diacanthaspis* the number of cephalic spines increases throughout development, but in the adult they are reduced to tubercles.

Lalicker (1935) has claimed that in the protaspid of a middle Cambrian trilobite the facial suture, palpebral lobes, and free cheeks are present before the eye appears on the test as a visual surface. Unfortunately, the free cheeks of the smallest stages of *Flexicalymene* and *Diacanthaspis* are not preserved, and hence the stage at which the visual surface of the eye first appears cannot be ascertained.

In the protaspid of *Flexicalymene* the palpebral lobes, and thus the nerve system of the eye if not the actual visual surface, are present on the dorsal surface close to the anterior margin. There is, then, from this collection "no evidence whatever of eyes in trilobites migrating from the ventral to the dorsal surface" (from discussion in Raw, 1927, p. 17). The comparatively large size of the eye, as measured by the size of the palpebral lobe, is notable in the protaspid and meraspid degrees.

The view most widely accepted by authors is that new segments of the trilobite are formed during growth at the anterior border of the last segment of the pygidium and detached forwards from the anterior border of the transitory pygidium to become freely articulating segments of the thorax. Jaekel and Richter have advanced evidence for believing that the budding place for new segments is between the thorax and pygidium. Stubblefield (1926) has brought forward convincing evidence in favor of the former hypothesis (see this same paper, pp. 365–366, for discussion and references on the origin and growth of the postcephalic segments). The development of the pygidium of *Ceraurus pleurexanthemus* also strongly supports the same view, the main spines being on the fifth segment of the smallest specimen, and moving forward with increas-

ing size until the adult position on the anterior segment of the pygidium is attained.

The transitory pygidia of *Ceraurus pleurexanthemus* are of the greatest interest, however, in that they show on the inner surface the development of the articulating half ring, the posterior doublure, and the appendifers (see text figs. 11–13). The articulating half ring and the posterior doublure develop together as one unit in the portion of the test between the anterior edge of the articulating furrow and the posterior edge of the axial ring of the next anterior segment. In the smallest transitory pygidia (text fig. 11), this area between the third and fourth segments is a narrow crescent, with a gentle slope along the anterior edge up to the axial ring of the third segment. The next anterior area is longer, with a very steep anterior slope. The area between the first and second segments is of the same length as the articulating half ring of the first segment, and the anterior edge is folded back to the axial ring of the first segment. The release of this first segment into the thorax is effected by the development of a suture along the rib furrows of the pleurae and around the anterior edge of the flat part of the crescentic area (text fig. 13). The segment released thus possesses a short posterior doublure, formed by the overfolded anterior edge of the crescentic area, and the segment which now becomes the anterior segment of the transitory pygidium has an articulating half ring formed by the flat part of the crescentic area.

The appendifers are developed in the fifth segment of the smallest transitory pygidium as low, rounded bosses at the junction of the axial and articulating furrows. In the succeeding more anterior segments the appendifers are progressively more strongly developed and situated a little farther within the articulating furrow, and in the anterior segment they are fully developed (text fig. 11).

Successively larger transitory pygidia show that the crescentic area never develops between the segment with the long pleural spines and the segment following it (text fig. 13). Thus in the smallest true pygidia this area is never present, and to this extent the formative zone ceases to be active in the true pygidium. Also, in the true pygidium the appendifers of the second segment are at the junction of the articulating furrow and the axial furrows, not within the articulating furrow as those of the first segment.

The suggestion made by Stubblefield (1926, p. 367), that the articular facet was present in a rudimentary condition when the segment was split away from the telson, and becomes truly functional when the segment reaches the fore part of the pygidium, seems therefore to be verified. Each segment of the transitory pygidium which is to become a thoracic segment develops progressively as it moves forward in the transitory pygidium from the telson to the thorax.

As has been noted by Shirley (1936, p. 398) the furrows in the glabella of many trilobites become deeper during development. This is true of *Flexicalymene*, *Diacanthaspis*, *Ceraurus*, and *Cryptolithus*, but the reverse is true of *Isotelus*. The meaning of this difference in families of trilobites is not clear.

Mode of life, enrollment, and protection.— The material includes three enrolled specimens of *Cryptolithus tesselatus*, one at meraspid degree 0, one at degree 2, and the third a large holaspid (pl. 75, figs. 5, 4, 23). The latter shows that the posterior and lateral margins of the pygidium, and the bent-down lateral extremities of the pleurae, fit closely against the inner edge of the lower lamella. The thickened anterior part of the latter fits against the margin of the pygidium and the lateral continuation of this thickening as a ridge between I_2 and I_3, dies out posteriorly as the pleural extremities of the anterior segments butt against the inner posterolateral margins of the lower lamella.

In the meraspid degree 0 specimen, the margin of the pygidium, semicircular in outline, fits against the inner edge of the lower lamella, the anterior part of which is thickened. The degree 2 specimen shows this same condition. These early meraspid specimens differ from the holaspid in that the outline of the pygidium and of the inner edge of the lower lamella is subsemicircular and not subtriangular, and the lower lamella itself is flat anteriorly and not V-shaped in cross section. It would seem, therefore, that during development, as the pygidium changes in outline from subsemicircular to subtriangular, so the outline of the inner

edge of the lower lamella anteriorly gradually becomes arched forwards beneath the glabella, the cross section becomes V-shaped, and a few pits of I_1 and I_2 become fused together.

Thus the importance of an exact and close fit of the test when enrolled throughout the meraspid and holaspid periods is emphasized. The only gap in this protection of the soft parts of the animal seems to be that between the axial ring of the first thoracic segment, which has no articulating half ring, and the occipital ring. Presumably the occipital spine protected this point. The enrollment of *Cryptolithus* may be closely compared with that of *Harpes*, as described by Richter (1920, pp. 204–205).

The cephalon of *Cryptolithus* seems to have rested on the lateral parts of the edge of the fringe, the anterior part being bent up (Størmer, 1930, p. 106), and on the genal spines. It may be noted that the latter would enable the cephalon to remain in the same plane relative to the sea floor whether the thorax and pygidium were enrolled or extended.

Flexicalymene protected itself by enrollment in a similar manner to *Cryptolithus*, the margin of the pygidium and the lateral extremities of the bent-down pleurae fitting inside the rolled anterior and lateral margin. Thus no spines are needed for protection, and the holaspid is without them.

The spines on the pygidium of *Ceraurus* and *Diacanthaspis* and the position of the hypostoma of the former prevented them from enrolling into a close-fitting ball, with the margin of the pygidium against the inner edge of the anterior margin of the cephalon (cf. Öpik, 1937, pl. 17, fig. 2), as was true of *Flexicalymene* and *Cryptolithus*. Presumably their spines protected them when they clung fast to the floor of the sea, as suggested by Richter (1920, pp. 34–35). Richter has further suggested (1920, pp. 32, 33) that the power of enrollment would presumably be valuable, if they were attacked while swimming, to enable them to close up and sink rapidly to the protection of the sea floor.

IV. CONCLUSIONS

The present study, together with a brief examination of silicified trilobites from lower horizons of the Ordovician, suggests the following conclusions.

In the early developmental stages of *Flexicalymene*, *Diacanthaspis*, and many other genera, the test is spiny. With increasing size the number of spines may be much greater, but they are in general reduced in length and may become short spines or tubercles, or they may be lost. Spininess may therefore be a primitive character in many families of trilobites. Other genera, such as *Cryptolithus* and other trinucleids, *Ampyx*, and *Lonchodomas*, seem to have a few stout spines on the test, e.g., the genal spines. The occipital spine of *Cryptolithus* appears and increases in size during development. Illaenid and asaphid trilobites seem to be smooth or with few spines at the earliest stages.

Paired spines have been observed on the tests of many trilobites in both developmental and adult stages. In view of the analysis made above of the spines on the test of *Diacanthaspis*, it may be that spines on the tests of other genera do not appear sporadically and are not without arrangement. Further, the arrangement on the cephalon may reflect the original segmentation.

The study of the protaspis of *Flexicalymene* and the smallest cranidia of *Diacanthaspis* yields evidence favoring the view that the eye of the trilobite belongs to the fifth segment of the cephalon.

The anterior pits of the axial furrows of *Ceraurus* and *Flexicalymene* support the hypostoma. The anterior pits of *Cryptolithus* may not function in this way. Many trilobites do not have the anterior pits. The function of these pits, therefore, may not always be the same, and they cannot necessarily be assumed to be the seat of attachment of the antennules. Hence it is not certain that they can be homologized with the postoral appendifers.

In *Ceraurus* and *Flexicalymene* the hypostoma is attached to the rest of the cephalon by the hypostomal suture and articulating joints between the anterior wings and the anterior pits. In both these genera there are connective sutures isolating an epistoma. In *Isotelus* and *Pseudasaphus* the hypostoma is attached at the hypostomal suture, and the anterior cephalic doublure is crossed by a

median suture. There are no anterior pits. Phacopids do not possess the connective or median sutures, and the anterior wings seem to be important in the attachment of the hypostoma. The nature and mode of attachment of the hypostoma of *Cryptolithus* and probably other trinucleids is uncertain. The evidence suggests that in many genera of trilobites the hypostoma was firmly fixed relative to the rest of the cephalon, and only small movement in one plane was possible. It may thus have served as an anchor and a protection for the soft parts enclosed within the anterior part of the glabella.

The appendifers of trilobites are developed to very differing degrees, and the meaning of these variations is unknown. In *Ceraurus*, the appendifers of the thoracic segments are apparently uniform in shape, but those of the first cephalic and first pygidial segments differ in being thickened at the extremity.

The articulating ring and posterior doublure of the axial ring of adjacent segments of *Ceraurus* develop together as a single fold in the transitory pygidium. When a segment is split off the latter to become a freely articulating member of the thorax, this fold is divided into its two component parts.

In certain families of trilobites, e.g. calymenids, trinucleids, raphiophorids, etc., the faculty of enrolling into a closely fitting ball is of importance. In other families, e.g. cheirurids, odontopleurids, no such close-fitting enrollment is possible.

The nature and course of the sutures on the ventral as well as the dorsal surface of the trilobite cephalon, the presence or absence of an epistoma, and the mode of attachment of the hypostoma, may perhaps be of fundamental importance in seeking a basis for a new classification of the trilobites. The changes which take place during ontogeny, especially in the cephalon, may afford further criteria, e.g. in *Isotelus* the glabellar furrows are lost early in the development, in *Diacanthaspis* and *Flexicalymene* they become deeper and longer, and new furrows develop; in *Flexicalymene* the posterior portion of the glabella increases in width; in *Diacanthaspis* a marked increase in length as well as width of the posterior part of the glabella and the occipital ring occurs. The importance of the investigation of the ventral surface of the trilobite test is emphasized, and modern techniques make such preparations possible in almost any matrix in which the fossil may be enclosed.

REFERENCES

BARRANDE, J., *1852*, *Système silurien de la Bohême*, vol. I. Prague and Paris.

BASSLER, R. S., *1915*, Bibliographic index of American Ordovician and Silurian fossils: *U. S. Nat. Mus., Bull.* 92.

CONRAD, T. A., *1841*, *New York Geol. Survey, Ann. Rept.* 5, pp. 25–57.

HALL, J., *1847*, *Paleontology of New York*, vol. 1.

JAEKEL, O., *1901*, Beiträge zur Beurtheilung der Trilobiten: *Deutsche geol. Gesell.*, Band 53, Heft 1, pp. 133–171.

KAY, G. M., *1937*, Stratigraphy of the Trenton group: *Geol. Soc. America, Bull.*, vol. 48, pp. 233–302.

KING, W. B. R., *1914*, A new trilobite from the Millstone grit of North Yorkshire: *Geol. Mag.*, dec. 6, vol. 1, pp. 390–394.

LALICKER, C. G., *1935*, Larval stages of trilobites from the Middle Cambrian of Alabama: *Jour. Paleontology*, vol. 9, pp. 394–399.

ÖPIK, A., *1929*, Über Muskelhaftstellen der Glabella von *Pseudasaphus tecticaudatus* Steinh. (Crust., Trilobita) und über die Funktion der Fazialsutur: *Naturf. Gesell. Univ. Tartu, Sitzungsber.*, Band 35, Heft 3, 4, pp. 1–17.

——, *1937*, Trilobiten aus Estland: *Univ. Tartu, Geol. Inst., Pub.* 52.

RAW, F., *1925*, The development of *Leptoplastus salteri* and other trilobites: *Geol. Soc. London, Quart. Jour.*, vol. 81, pp. 223–324.

——, *1927*, The ontogenies of trilobites and their significance: *Am. Jour. Sci.*, vol. 14, pp. 7–35; 131–149.

RAYMOND, P. E., *1914*, Notes on the ontogeny of *Isotelus gigas* Dekay: *Harvard College, Mus. Comp. Zoology, Bull.*, vol. 58, no. 5, pp. 247–263.

——, *1917*, Beecher's classification of trilobites, after twenty years: *Am. Jour. Sci.*, vol. 43, pp. 196–210.

——, *1920*, The appendages, anatomy, and relationships of trilobites: *Connecticut Acad. Arts and Sciences*, vol. 7.

——, and BARTON, D. C., *1913*, A revision of the American species of *Ceraurus*: *Harvard College, Mus. Comp. Zoology, Bull.*, vol. 54, no. 20, pp. 525–543.

——, and NARRAWAY, J. E., *1910*, Notes on Ordovician trilobites, III: *Carnegie Mus. Annals*, vol. 7, no. 1, pp. 46–59.

REED, F. R. C., *1925*, The classification of the *Acidaspidae*: *Geol. Mag.*, vol. 62, pp. 416–430.

RICHTER, R., *1920a*, Von Bau und Leben der Trilobiten, II: *Senckenbergiana*, Band 2, Heft 1, pp. 23–43.

——, *1920b*, Beitrage zur Kenntnis Devonischer Trilobiten, II: *Senckenburg. Naturf. Gesell., Abh.*, Band 37, pp. 179–218.

RUEDEMANN, R., *1912*, The Lower Siluric shales of the Mohawk Valley: *New York State Mus., Bull.*, no. 162.

SHIRLEY, J., *1936*, Some British trilobites of the family Calymenidae: *Geol. Soc. London, Quart. Jour.*, vol. 92, pp. 384–422.

STØRMER, L., *1930*, Scandinavian Trinucleidae: *Norske vidensk.-akad. Oslo, Schr., I Math. Nat. Kl.* no. 4, pp. 1–111.

——, *1939*, Studies on trilobite morphology, Pt. I: *Norsk. geol. tidsskr.*, vol. 19, pp. 143–273.

STUBBLEFIELD, C. J., *1926*, Notes on the development of a trilobite, *Shumardia pusilla* (Sars): *Linnean Soc. London, Jour., Zoology*, vol. 36, pp. 345–372.

——, *1936*, Cephalic sutures and their bearing on current classifications of trilobites: *Biol. Rev.*, vol. 11, pp. 407–440.

SWINNERTON, H. H., *1915*, Suggestions for a revised classification of trilobites: *Geol. Mag.*, dec. 6, vol. 2, pp. 487–496; 538–545.

VOLBORTH, A. v., *1863*, Russischen Trilobiten: *Acad. Imp. Sci. St. Petersbourg, Mém.*, t. 6, no. 2, pp. 1–47.

WALCOTT, C. D., *1879*, *New York State Mus., Ann. Rept.* 31.

WARBURG, E., *1925*, The trilobites of the *Leptaena* limestone in Dalarne: *Geol. Inst. Univ. Upsala, Bull.*, vol. 17.

——, *1934*, On the structure of the occipital ring of the Odontopleuridae: *Arkiv für Zoologie*, Stockholm, bind 25, no. 9.

WHITTARD, W. F., *1938*, The upper Valentian trilobite fauna of Shropshire: *Annals and Mag. Nat. History*, ser. 11, vol. 1, pp. 85–140.

WHITTINGTON, H. B., *1940*, On some Trinucleidae described by Joachim Barrande: *Am. Jour. Sci.*, vol. 238, pp. 241–259.

——, *1941*, The Trinucleidae, with special reference to North American genera and species: *Jour. Paleontology*, vol. 15, pp. 21–41, pls. 5, 6.

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DEVELOPMENT OF THE MIXOCHOANITES

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ABSTRACT—Mixochoanitic cephalopods from the Chazyan of the Champlain valley, constituting three genera, supply the first evidence of the group in the Lower Ordovician and supply evidence by which the Mixochoanites can be traced to their origin in slender longiconic cephalopods. Ellipochoanitic cephalopods are briefly discussed, and new morphological groups are outlined to replace the formerly used Orthochoanites and Cyrtochoanites. From the second of these groups, the suborthochoanitic cephalopods, the Mixochoanites were developed. The earliest distinctive feature of the line was natural truncation of the shell. Gibbosity of the anterior end of the shell is a Middle Ordovician development, followed by the appearance of the ascoceroid septum in the Upper Ordovician. Study of the ascoceroid conchs shows that one main line instead of two lines is involved. In the revised classification, the family Schuchertoceratidae is eliminated and a new family Hebetoceratidae is proposed for primitive Mixochoanites. A unique feature of the group is the elimination of septa at the base of the mature individual and subsequent reduction of free siphuncular segments. By this means the gradual change from orthochoanitic to cyrtochoanitic is replaced by an abrupt transition in younger genera.

INTRODUCTION

THE RELATIONSHIP of that group of anomalous cephalopods for which Hyatt proposed the name Mixochoanites is a problem which has given rise to some exceedingly diverse suggestions by various investigators. The history of investigation has been summarized by Lindström (1890) and more fully by Miller (1932) and need only be outlined here. Barrande, who described the first genera known, regarded them as constituting a group equivalent to that embracing all other genera of nautiloids. Other investigators put forward other suggestions without, however, much amplification of their reasons for doing so; and at various times the ascoceroids were placed with the brevicones, orthoceracones, gyroceracones, and cyrtoceracones. Eichwald (1860) placed them with *Nothoceras* and *Sepia*, which today seems an anomalous combination. Lindström studied the group in detail and regarded it as allied to *Cyrtoceras* and to breviconic cephalopods.

Hyatt (1900) regarded the sudden change of the siphuncular segments from orthochoanitic to cyrtochoanitic as the essential important feature. On the basis of this abrupt change, now known to be confined to only the most specialized of the Mixochoanites, the ascoceroids could not be placed in either of the two major groups of ellipochoanitic cephalopods, the Orthochoanites and Cyrochoanites. He therefore erected a third group for which he proposed the name Mixochoanites. He did not discuss the origin of the group or its relationship with other cephalopods and apparently considered it a specialization of its own, not closely related to any other known cephalopods. His conclusion was justified by the forms known at that time.

For the next thirty years contributions to our knowledge of the group were very largely confined to descriptions of new species. The most significant advance in this period is an increase in knowledge of Middle and Upper Ordovician forms, largely due to the investigations of Foerste. Miller (1932) presented a very lucid summary of the group, describing and illustrating all genera, proposing several new ones, and listing the known species. Further, he limited the group, removing from it such genera as the little known *Mesoceras* Barrande (1877) the problematic cephalopod *Volborthella* Schmidt (1884) and the coiled *Ophioceras* Barrande (1865). The oldest forms then known were of Middle Ordovician age. The part of the shell retained in the mature individual was strongly gibbous in these genera and was more suggestive of breviconic cephalopods than were the younger ascoceroids. Miller therefore suggested that the Mixochoanites probably arose from a brevicone, perhaps some *Oncoceras*-like form, and presented a revised classification and phylogeny of the group.

The writer, while investigating the nautiloid fauna of the Chazy limestone of the Champlain valley, came upon primitive mixochoanitic cephalopods which formed the beginning of this investigation. These constitute three new genera, *Montyoceras*, *Hebetoceras* and *Ecdyceras*, which are described below together with their genotypes and such few additional species as seem to be of particular significance. *Hebetoceras* is known from the genotype and one additional species, which can be referred to the genus only with some doubt. *Ecdyceras* is at present monotypic. *Montyoceras*, however, is represented by a variety of species, only three of which are included in the present work. Others will be discussed in the forthcoming study of the Chazy Nautiloidea.

Not only do these Chazyan Mixochoanites constitute the oldest members of the group now known, but they present new evidence concerning the origin of the suborder and its development. In connection with the discussion of origin, it is necessary to review briefly the problem of the classification of the ellipochoanitic cephalopods, a grouping which embraces the Mixochoanites, with particular reference to new groupings that are believed to approximate the genetic relationships more closely than those proposed by Hyatt some forty years ago.

DIVISIONS OF ELLIPOCHOANITIC CEPHALOPODS

Those cephalopods in which the siphuncular segment is made up of a short septal neck supplemented by a connecting ring are termed ellipochoanitic. The term is used now only in a descriptive sense, but it finds its origin in Hyatt's (1884) original division of the Nautiloidea into Holochoanoidea and Ellipochoanites. Later Hyatt (1900) discarded the Ellipochoanoidea, substituting instead four groups, the Orthochoanites, Cyrtochoanites, Mixochoanites and Schistochoanites. The first two divisions are particularly important, for they contain the majority of nautiloid genera, while the other groups are small and were erected for aberrant and peculiar forms. The Orthochoanites constitute those cephalopods in which the septal neck is short and parallel to the axis of the conch and the connecting ring is more or less tubular. In the Cyrtochoanites are placed cephalopods in which the septal neck is definitely recurved and the siphuncular segment is more or less expanded.

The distinction between orthochoanitic and cyrtochoanitic structure is not always an easy one. There are too many intermediate phases, and in the past there has been no wide agreement as to how strongly the septal neck must be recurved before it passes the very tenuous boundary between the two groups. Of recent years more attention has been given to the internal structure of nautiloids, and the difficulties presented by forms which might be placed in either group have become more apparent. Further, recent studies have led various investigators to consider such a dichotomous division of ellipochoanitic cephalopods as inadequate. Teichert (1933) has shown that the Actinoceroidea are not closely related to other cyrtochoanitic cephalopods, and Flower (1939) found that the cyrtochoanitic family Pseudorthoceratidae was derived from Silurian orthochoanitic forms and was totally independent of other and older groups of cyrtochoanitic cephalopods.

In treating the Ozarkian and Canadian cephalopods Ulrich and Foerste (1933) remarked that differentiation between orthochoanitic and cyrtochoanitic structure did not appear until Ordovician time. Perhaps it is not surprising, then, to find that the differentiation between the groups is still very poor in the Lower Ordovician, so poor, in fact, as to be practically useless. Though some genera are clearly orthochoanitic and others are as clearly cyrtochoanitic, intermediate phases are particularly prevalent. The writer found that it was impossible to fit the Chazyan genera accurately into Hyatt's scheme, but instead they appeared to fall naturally into the following five morphological groups:

I. Orthochoanitic cephalopods with perfectly cylindrical siphuncular segments.

II. Suborthochoanitic cephalopods, in which the septal necks are straight or nearly so, but the connecting rings are slightly curved, producing slightly convex siphuncular segments.

III. Cyrtochoanitic cephalopods with relatively small and slender siphuncular segments for the most part, which become suborthochoanitic when traced adapically.

The ontogeny here seems to imply that these forms originated from those of the above group.

IV. Cyrtochoanitic cephalopods with relatively slender segments, the very earliest stages still unknown, but with the earliest-known segments cyrtochoanitic. The outline of the segments is simplified adorally; they become more and more slender until a suborthochoanitic condition is attained in the latest part of the phragmocone.

V. Apparently primitively cyrtochoanitic cephalopods in which the siphuncular segments are broadly expanded in the earliest-known stage.

These groups are clearly morphological and are not given taxonomic names. Some are clearly not genetic groups and are composed of recognizably distinct elements. Some others probably represent closely knit genetic groups, but it is felt that the proposal of names for these units should await further study and should preferably be delayed until it is possible to define a series of equivalent groups embracing all stenosiphonate ellipochoanitic cephalopods.

In view of the slight structural differences involved in the distinction of the orthochoanitic and suborthochoanitic cephalopods as defined above, they are remarkably distinct in the Chazyan, and also, from the rather limited observations of the writer, in the Beekmantown as well. This does not hold, however, for later Paleozoic cephalopods. Certainly when both types of outline are found in such a distinctive genus as *Harrisoceras* Flower (1939a) of the Silurian, it is evident that while the divisions may represent distinct genetic entities in the Ordovician, their description as taxonomic groups will require further emendation. It is not as yet certain which of these groups of the Ordovician gave rise to the annulosiphonate and related orthoceracones of the Silurian and Devonian. It seems likely, however, in view of the absence of cameral deposits in the Ordovician suborthochoanitic cephalopods, that these younger forms characterized by an abundance of such structures probably were derived from the strictly orthochoanitic forms.

Orthochoanitic forms with perfectly cylindrical siphuncles constitute a variety of genera in the Chazyan and show such a diversity of form as to suggest that they were differentiated long before. Probably many Canadian genera will eventually be placed here also. Smooth and ornamented orthoceracones are represented, a variety of cyrtoconic forms mostly constituting undescribed genera, and a large number of coiled genera constituting the Tarphyceratida of Hyatt. Clearly if this is a genetic group its origin must be sought in much earlier strata, for the Tarphyceratida are still distinct in the Lower Canadian.

The suborthochoanitic cephalopods represent a much smaller group. Only three longiconic genera are known, which appear in the Chazyan: *Sactorthoceras* Kobayashi (1934), *Sigmorthoceras* Kobayashi (1934), and *Centroonoceras* Kobayashi (1934). *Montyoceras*, described below, may be placed here, as it retains the suborthochoanitic condition throughout life, though it is the first of the true Mixochoanites. Other possible members of the group are discussed below in connection with ancestral and primitive types of the Mixochoanites.

The additional groups (III–V), are not essential for an understanding of the relationship of the Mixochoanites but are briefly outlined here for the sake of completeness.

The third group, consisting of secondarily cyrtochoanitic cephalopods which can be traced to suborthochoanitic forms by their ontogeny, constitute several families including the Oncoceratidae, Tripteroceratidae, and at least one actinosiphonate group, the Diestoceratidae. These families, appearing simultaneously, appear to represent parallel and independent offshoots from group II rather than a single genetic unit. It is suspected that many other groups of Paleozoic cyrtochoanitic cephalopods, particularly among the Ordovician cyrtoceracones and brevicones, may prove to have similar suborthochoanitic early stages and to represent parallel or related stocks.

The fourth group contains only a small number of genera of rather inadequately known orthoceracones and cyrtoceracones. By the heavy cameral deposits and the relatively slender condition of the siphuncular segments these genera are tentatively assigned to the family Stereoplasmoceratidae Kobayashi. The origin of the group is uncertain, as the earliest ontogenetic stages are

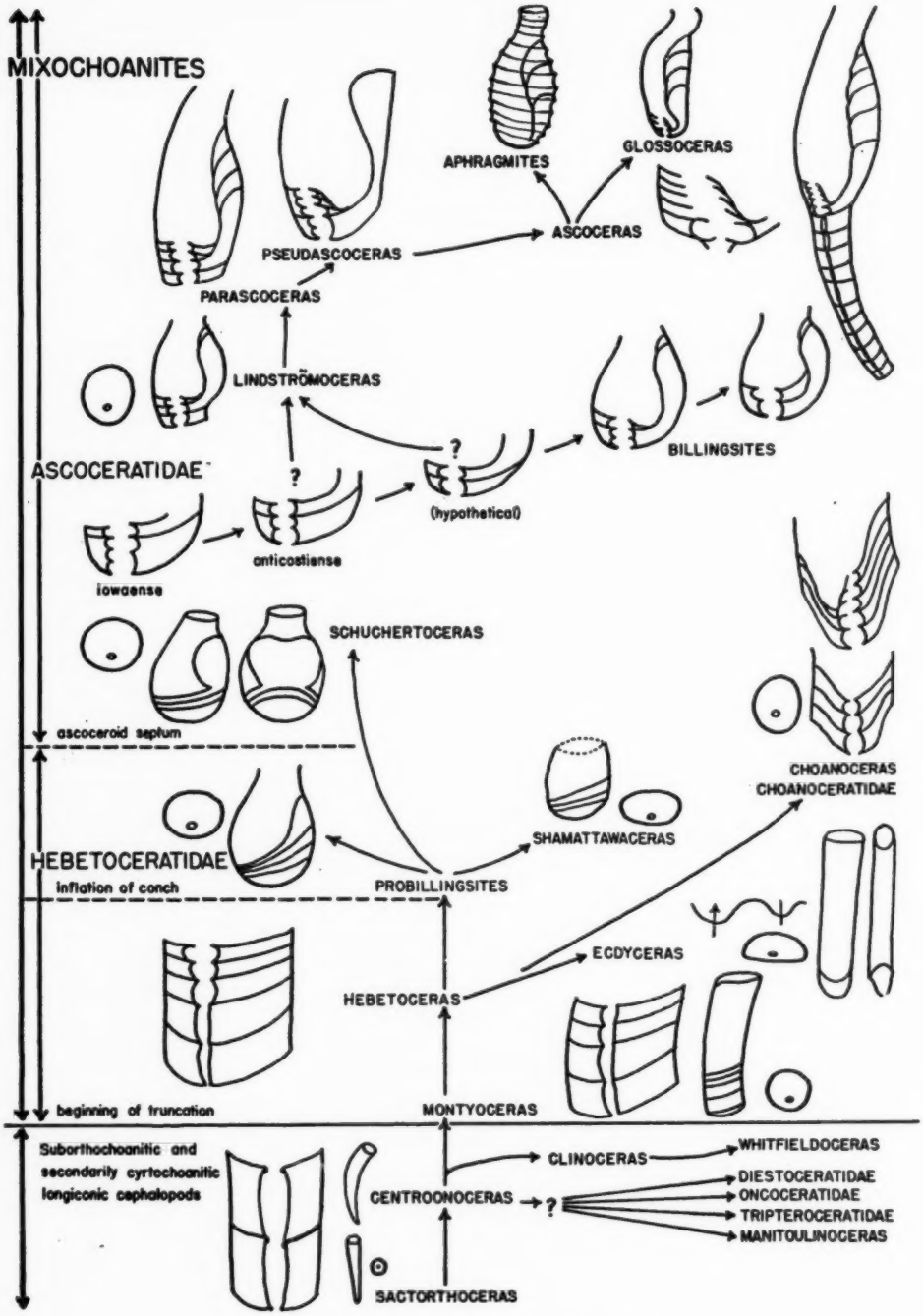


FIG. 1—Evolution of the Mixochoanites.

unknown; but it is strongly suspected that it also may be of suborthochoanitic origin. The present available structural evidence shows that this differs from the preceding group in that the ontogenetic sequence is directly reversed.

The last group, constituting the ancient and presumably primitive cyrtochoanitic cephalopods is clearly made up of two unrelated elements. One is the superfamily Actinoceroidea, which is not closely related to other cyrtochoanitic cephalopods and as Teichert (1933) has suggested may be more closely related to the Endoceroidea than to any other group of cephalopods. In addition, there is a group of cephalopods which agree with the Actinoceroidea in having broad and strongly cyrtochoanitic siphuncular segments, but in which the apical end is very small, and the siphuncle is either empty or lined with a continuous deposit. Radial canals are always absent. This group is represented by *Cyrtactinoceras boyci* (Whitfield) and *C. champlainense* Ruedemann in the Chazyan. These species are not properly referred to the Silurian genus *Cyrtactinoceras*, and a new genus will be erected for them at another time. The group as a whole will require extensive treatment, and discussion of it must be deferred. At the present time there is no evidence to connect this with the Actinoceroidea, and the small apical ends suggest that this is probably actually a primitive cyrtochoanitic stenosiphonate group.

DEVELOPMENT OF THE MIXOCHOANITES

A. Ancestral and primitive types.—The development of the main line of the Mixochoanites can be traced through a number of stages, each of which is represented by a distinct genus.

1. The logical beginning of the series consists of a suborthochoanitic orthoceracones, the simplest members of group II outlined above. For such forms the generic name *Sactorthoceras* Kobayashi (1934) is being used, although with some slight restrictions in scope, confining it to cephalopods without cameral deposits. The surface is smooth, the section circular, and the suborthochoanitic siphuncle is central in position or nearly so. (Text fig. 1.)

2. *Centroonoceras* Kobayashi (1934) represents a slight advance, the essential feature being the beginning of curvature. The section is subcircular or, rarely, slightly depressed, and the siphuncle is still subcentral in position.

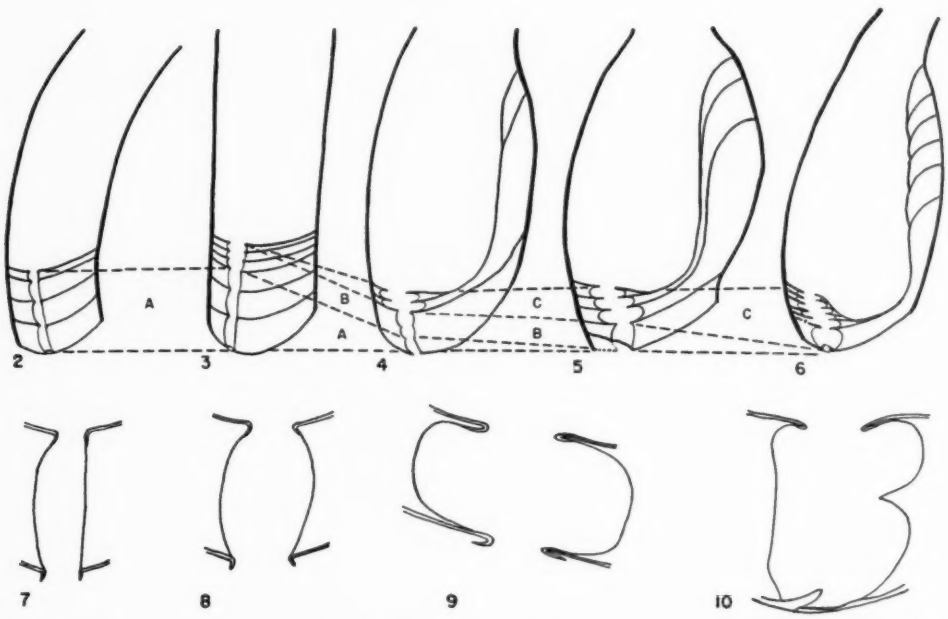
3. *Montyoceras* Flower, n. gen. (text figs. 1, 2), represents a considerable advance. The section is depressed, the siphuncle lies well ventrad of the center, the sutures tend to slope orad from venter to dorsum, and the septum is asymmetrically curved in the vertical plane, being more strongly arched ventrally than dorsally. The siphuncular segment is biconvex in horizontal section, but in vertical section it is planoconvex, that is, with the dorsal side straight, the ventral side slightly expanded within the camerae. In

EXPLANATION OF TEXT FIGURE 1

FIG. *1*—Diagrammatic representation of the evolution of the mixochoanites, showing essential structural changes. All vertical sections oriented with venter at left. Ancestral longiconic forms include the orthoconic *Sactorthoceras* and the cyrtoconic *Centroonoceras*. *Montyoceras* shows a depressed cross section, ventrally steepened septa, and planoconvex siphuncular segments. An internal mold of a mature individual is shown laterally. *Hebetoceras* is straight and develops biconvex segments. Septa are more strongly curved. *Ecdyceras* is specialized in section and sutures. Ventral and lateral view show the subconical septa. *Choanoceras* differs in the compressed section. Two vertical sections show the siphuncle and septa in early and late stages of growth. *Probillingsites* and *Shamattawaceras* are depressed gibbous forms. The selected illustrations show extremes in depression of section, gibbosity of conch, and obliquity of sutures. *Schuchertoceras* is depressed. Lateral and dorsal views show the ascoceroid septa above the basal septum. The species show progressive reduction in prebasal siphuncular segments leading to *Billingsites*. Two hypothetical stages are inserted. *Lindstroemoceras* differs mainly in the compressed section. The conch is still gibbous, but the aperture is slightly produced. *Parascoceras* differs only in the more slender form and the more produced aperture. The basal septum is lost in *Pseudoscoceras*, only the basal part of which is shown. One of the free segments is eliminated in *Ascoceras*. *Glossoceras* is modified mainly in the tubular form of the living chamber, which is bent around the dorsal camerae. *Aphragmites* differs from *Glossoceras* mainly in the development of annuli.

this genus are found the essential features of the septa and siphuncle, which are retained in the early longiconic portion of all ascoceroids. In addition, natural truncation of the conch is developed in this genus and is accompanied by the closure of the apical end of the siphuncle by a small lens-shaped plate. Gerontic camerae are markedly shortened, as in most nautiloids, but there is no gerontic

the position of the siphuncle, which is assumed to be ventral, as there is no hyponomic sinus. There is no real evidence supporting this orientation, and it appears probable that the position of the shell has been misinterpreted, and that the siphuncle is actually dorsal in position. The hyponomic sinus in *Montyoceras* leaves little cause to question the orientation in that genus. If



FIGS. *2–10*—Form, development and reduction of stages of siphuncular outline in the Mixochoanites. *1–4*, Showing the tachygenetic development of cyrtochoanitic segments. *4–6*, showing the progressive loss of ontogenetic and phyletic stages. *2*, *Montyoceras*. *3*, *Hebetoceras*. *4*, *Schuchertoceras iowaense*. *5*, *Lindstroemoceras*. *6*, *Ascoceras*. *7*, Planoconvex segment, A of *2–6*. *8*, Biconvex segment, B of *2–6*. *9*, Moniliform segment, C of *2–6;* D, Apparent retention of planoconvex outline in basal part of *Pseudoscoceras*, also showing the apparent closure of the apex of the siphuncle. (*4* After Miller; *5*, *6* and *9*, *10* after Lindström.)

modification of septal curvature or siphuncular outline such as is found in more specialized forms.

Possibly simpler types bridging the gap between *Centroonoceras* and *Montyoceras* will be found. One such possible connecting link, though with some specializations of its own is the genus *Clinoceras* Maeske (1876, see also Foerste, 1926). The siphuncular outline is planoconvex as in *Montyoceras*, but the orientation is purportedly reversed, with the straight wall nearest the wall of the conch. Orientation is apparently based on *Clinoceras* is oriented on the basis of the similarity of its siphuncular structure to *Montyoceras* it is exogastrically curved, though only very slightly, and differs from *Montyoceras* mainly in the simpler sutures, the longiconic condition of the shell, and the marked contraction of the entire shell, externally as well as internally, at the region just before the aperture.

Other possible relatives constituting cyrtoceracones of depressed section, ventral siphuncle, and longiconic conch have for the most part more expanded siphuncular seg-

ments and occur in somewhat younger strata. *Manitoulinoceras* (Foerste, 1924) is a typical example of this group. Representatives of this radicle still await discovery in the Lower Ordovician.

4. *Hebetoceras* Flower, n. gen., (text figs. 1, 3) differs from *Montyoceras* in the gerontic development of the septa and siphuncle. The anterior camerae of a mature individual are more contracted. The gerontic septa become less strongly arched, and the siphuncular segments in these camerae become first biconvex and then increasingly broader. The septal necks become recurved for the first time, and the genus is mixochoanitic in the original sense of the word, even though the condition is attained gradually.

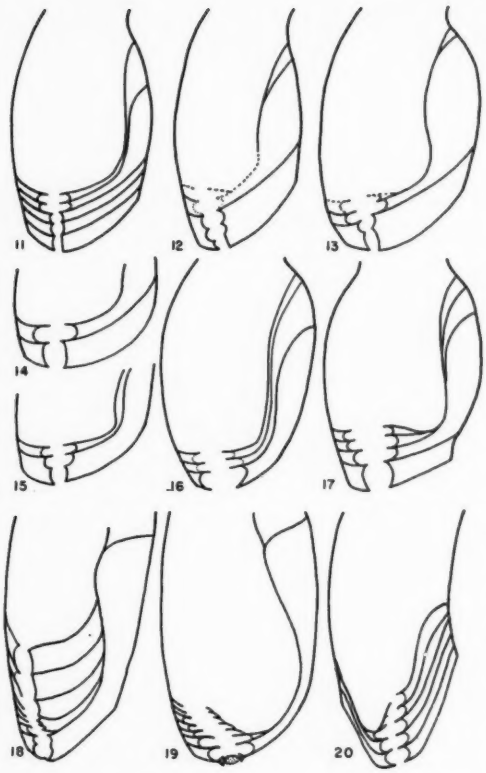
5. In *Probillingsites* and *Shamattawaceras* the adoral part of the conch, that retained in the mature individual, has become inflated, and the gerontic sutures show a marked tendency to bend orad on the dorsal side of the shell. In these genera, which may possibly intergrade, *Shamattawaceras* is the more strongly depressed in section, has simpler sutures, and is less inflated in general than *Probillingsites*. The condition of the sutures varies strongly in *Probillingsites* from the condition found in *P. welleri* Foerste, where they are relatively simple, to that found in *P. primus* (Fritz), where the sutures slope so markedly orad on the dorsum that the ascoceroid affinities of the conch are very evident. Unfortunately nothing is known of the condition of the siphuncle in either genus. The meager material available for the present study failed to yield any trace of internal structure. Quite possibly the condition of the siphuncle is very close to that represented in text figure 11, which is the hypothetical ancestral type of *Schuchertoceras*.

B. Development of the Ascoceroids.—The feature that separates the ascoceroids proper from the primitive members of the Mixochoanites is found in the development of the sigmoid ascoceroid septum. This is strongly bent forward on the dorsum and develops a complex suture. Accompanying the ascoceroid septum is the development of a more markedly expanded siphuncular segment, one which is very broadly expanded, usually with the brims recumbent or at least strongly recurved, and with the connecting ring adnate to the septum, at least at its adapical end. This segment, which, for short, will be referred to as the ***moniliform segment***, is invariably found in association with the ascoceroid septum. Normally it is greater in height than in length, and the first of the segments normally differs from the others in being somewhat longer, with the height somewhat less and the breadth considerably greater, as is shown clearly by Lindström's (1890) careful sections and illustrations. Another significant feature of the ascoceroids is the fusion of septa dorsad of the siphuncle, a condition which continues over the projecting lobes of the septa nearly to the shell wall, where the septa again become free and form distinct camerae.

Within the ascoceroids it is possible to recognize two groups, those with or without a ***basal septum***. This term was proposed by Miller (1932) for a normal and a simple nautiloid septum between the septum of truncation and the first ascoceroid septum. Such a septum is found in *Schuchertoceras* Miller, *Lindstroemoceras* Miller, and *Parascoceras* Miller and is obsolete in *Pseudascoceras* Miller. In contrast, *Billingsites* Hyatt, *Ascoceras* Barrande, *Glossoceras* Barrande and *Aphragmites* Barrande lack all trace of the basal septum.

Miller (1932) used these groups as families, retaining for one the family name Ascoceratidae of Barrande and proposing for the other the new family Schuchertoceratidae. Further, he regarded these families as independent developments from *Probillingsites*. This hypothesis requires so many and such unusual parallel developments that there is reason to wonder whether some other explanation is not possible.

On superficial examination it might appear possible that the fusion of adoral septa might have taken place several times independently in the Mixochoanites, in *Choanoceras*, *Schuchertoceras* and *Billingsites*. However, closer examination shows that the resemblance between *Choanoceras* and a true ascoceroid condition is really very superficial, whereas the condition of the ascoceroid septa is identical in *Schuchertoceras* and *Billingsites*. Further, these coexisting genera are identical externally except for the difference supplied by the development of a basal



FIGS. *11–20*—Vertical sections of mixochoanitic cephalopods. Venter on left.

11—Hypothetical ancestor of *Schuchertoceras* with prebasal septa retained.

12—*Schuchertoceras iowaense*. (After Miller) showing three prebasal segments.

13—*Schuchertoceras anticostiense*. (After Foerste) showing two prebasal segments.

14—Hypothetical *Schuchertoceras* with one prebasal segment.

15—Hypothetical *Billingsites*. Basal septum lost, but its segment is retained in outline.

16—*Billingsites*.

17—*Lindstroemoceras*, showing condition similar to that of *14*. (After Lindström.)

18—*Pseudascoceras* showing retention of two siphuncular segments at base, reflecting ancestry. Also the anomalous condition of the latest siphuncular segments and septa, essentially a return to the condition of the longiconic part of the shell. (After Lindström.)

19—Base of *Ascoceras manubrium* (after Lindstrom) showing apical plate held by processes of septa.

20—*Choanoceras*. (After Lindström). Note that fusion of gerontic septa lies ventrad of the siphuncle in this genus.

septum in *Schuchertoceras*. Indeed, the genera were originally separated on this basis. Such internal differences as exist have to do with the greater number of siphuncular segments preserved in *Schuchertoceras*, together with the ontogenetic stages which are thus represented. These are omitted in *Billingsites*. Tracing the development of the families farther, it is found that out of the short gibbous depressed forms of the Upper Ordovician there are developed more slender compressed forms with produced apertures; and finally the peculiar collarlike structure in the basal septum, probably a specialization to facilitate the closure of the apex of the siphuncle following truncation. These developments are contemporaneous and identical and indicate strongly a single rather than two parallel genetic lines.

Comparison of species of *Schuchertoceras* shows indications of an orthogenetic trend which serves as the basis of another explanation for the known facts. In *Schuchertoceras iowaense* Miller (text fig. 12,) three siphuncular segments lie between the septum of truncation and the basal septum. These show by their outline the addition of two prebasal septa. Whether this reflects the ontogeny or the phylogeny is not absolutely certain. Miller has suggested that the absence of these septa might be due to resorbtion. This is supported by a specimen figured by Barrande (1877, pp. 98, 99, pl. 491, figs. 3–7) retaining two septa previous to the ascoceroid septum in *Parascoceras fistula*. The specimen may, as Miller (1932, p. 34, footnote) points out, be abnormal. The problem is difficult to solve because of the extreme rarity of individuals representing stages of growth just preceding the secretion of the basal septum. Whether such prebasal septa are formed in the development of the individual or not, there is no reason to doubt that the retention of these segments in *Schuchertoceras iowaense* reflects a more primitive ancestral condition in which such septa were not resorbed. Such a hypothetical ancestral type is shown in section in text figure 11. This may be an ascoceroid type that still awaits discovery. It is equally possible that the stage retained in *Schuchertoceras* by the retention of these siphuncular segments goes back to a preascoceroid phase, and that the ancestral condition shown in figure 11 is

really that of *Probillingsites* preceding the perfection of the sigmoid septum. *S. iowaense* preserves the planoconvex segment in the extreme base of the mature part of the phragmocone. Elsewhere in the genus, so far as known, this stage is not preserved in the mature individual, though there can be little doubt that it was developed in the slender cyrtoconic part, which, rather strangely, has not been recognized for any of the Middle or Upper Ordovician Myxochoanites.

Schuchertoceras anticostiense (Billings, 1862) (text fig. 13), the type of the genus, represents a more advanced condition, for it has only two prebasal siphuncular segments, and both are of the biconvex form. The planoconvex stage is omitted in the mature individual, though it was probably retained in the longiconic part of the shell, which was lost in the adult and is still unknown for the species. If this is a real reduction of septa and siphuncular segments, it is to be expected that the series may extend even farther. Its next step is found in the genus *Lindstroemoceras* Miller (1932), of the lower Middle Silurian, in which only a single siphuncular segment, and that biconvex, is found between the basal septum and the septum of truncation. Other specializations of the genus have to do with form and ornament. The conch is faintly compressed, and the aperture is somewhat more produced than before, but the shell is still gibbous as in *Schuchertoceras*. The surface has developed transverse ornament to a point at which transverse lirae and striae develop into an annulated exterior. *Parascoceras* Miller (1932) is internally identical with *Lindstroemoceras* but shows progress in the more slender form of the conch, the more compressed section, and the more strongly produced aperture. Existing with this genus and very similar to it in form, is *Pseudascoceras* Miller (1932). We have seen that in *Schuchertoceras* the disappearance of septa, at least in the mature individual, precedes the omission of siphuncular segments. In *Pseudascoceras* (text fig. 18), the basal septum has been lost, but the two siphuncular segments outlined apicad of the first ascoceroid septum show evidence of its former presence. Restoration of the missing septum shows that the first siphuncular segment is planoconvex though broader than usual, whereas the second is moniliform rather than biconvex. This suggests that here the planoconvex outline of the early stages has been pushed through into the mature individual, from which it was banished in the Ordovician *Schuchertoceras*. On the other hand, it may be simply an elimination in part of the division between the two siphuncular segments, which are no longer structurally necessary. Certainly the presence of the planoconvex segment is a definite reappearance here, and one for which there appears to be no good explanation in the phylogeny. (text figs. 10, 18.)

Continuation of the reduction series already demonstrated will result in a form differing from *Pseudascoceras* in the retention of only one siphuncular segment between the ascoceroid septum and the segment of truncation. This is *Ascoceras*, and, if the series is correct, *Ascoceras* is derived in this way rather than from *Billingsites* (text figs. 6, 19). The two additional genera of the ascoceroids of the Silurian, *Aphragmites* and *Glossoceras*, are internally identical with *Ascoceras*. *Aphragmites* is distinguished by the development of an annulated exterior; *Glossoceras* by the development of an extremely slender form (text fig. 1).

In the above series it is possible to trace a development from *Schuchertoceras* to *Ascoceras* on the basis of known genera and species. A similar independent development may have led to *Billingsites*, but evidence for or against it is lacking at present. Nevertheless it seems reasonable to assume that the reduction series shown in the only two species of *Schuchertoceras* that are known internally may easily have continued farther in typical Ordovician *Schuchertoceras*. Certainly there is no reason to believe that the reduction of the prebasal siphuncular segments from two to one was necessarily delayed until the development of *Lindstroemoceras* of the Silurian, which is specialized in other ways as well. Postulating such a stage in *Schuchertoceras* (text fig. 14), the next step in the reduction series involves the loss of the basal septum, as in the transition from *Parascoceras* to *Pseudascoceras*. Here, however, the change involves a transition from *Schuchertoceras* to a form which would be identified as a *Billingsites*. No *Billingsites*

having two segments is known; should one be found, the erection of a new genus for its reception might be justified. However, we have no assurance that this condition does not exist in some known species now placed in *Billingsites* (text fig. 15). Of the various species of the genus only one has been sectioned for siphuncular stages with any success; this shows the condition represented in text figure 16, which is comparable to *Ascoceras*.

Evaluation.—The phylogenetic scheme presented above offers a sharp contrast to the one previously proposed by Miller. Neither can be considered as proved conclusively to the exclusion of the other, therefore it remains to summarize briefly the reasons for and against the two separate beliefs.

It has already been pointed out that the recognition of two distinct families, the Schuchertoceratidae and Ascoceratidae, according to Miller's scheme requires remarkable contemporaneous parallel development, first in the appearance of the ascoceroid septum in the Upper Ordovician. This is followed in Lower and early Middle Silurian time by the development of a compressed section, the production of the aperture, and finally by the development of the collar in the basal septum. The series of contemporaneous parallelisms in two families is too remarkable to be accepted as long as other possibilities remain which do not require such remarkable isomorphism.

However, combinations, of characters are such that in erecting a new plan of development a new isomorphic series is built up, this time dealing with disappearance of septa followed by elimination of siphuncular segments from the base of the mature part of the conch. Such a series has already been demonstrated in part, namely from *Schuchertoceras* to *Pseudascoceras*, and *Ascoceras* is the logical end of this series. The reduction was already at work within the genus *Schuchertoceras*, as is shown by the demonstrable reduction of three prebasal segments of *S. iowaense* to two in *S. anticostiense*. The lack of supporting evidence showing the progression further to true *Billingsites* is not conclusive. The evidence which exists is based upon the only two species and specimens of *Schuchertoceras* that have yielded any trace of the siphuncle upon sectioning and only one species and one specimen show the condition in *Billingsites*.

The alternate hypothesis requires that the ascoceroid septum be developed twice independently out of *Probillingsites* in the contemporaneous genera *Schuchertoceras* and *Billingsites*. In view of the complexity of the ascoceroid septum, which is not duplicated anywhere except in these genera, which are obviously both related, too much is being required of the concept of isomorphism. Therefore it remains to develop one genus from the other. It is not difficult, in view of the Chazyan forms showing that the early siphuncular segments of *Schuchertoceras* are recapitulatory in their significance, to realize that this genus is primitive in the retention of such stages, while *Billingsites* is specialized by the omission of ontogenetic stages.

C. Early aberrant offshoots.—Having traced the main line of the Mixochoanites, namely that leading to the ascoceroids, it remains to consider two other genera with reference to this scheme. These are *Ecdyceras* Flower, n. gen., described below, a genus of the Chazyan, and *Choanoceras* Lindström (1890), of the Middle Silurian.

Ecdyceras, known from a single species from the Middle Chazyan of the Champlain valley, appears to be a specialization derived from *Hebetoceras* Flower, n. gen. It resembles that genus in the straight form of the conch, the depressed section, the deeply curved septa, and the position of the siphuncle. As the gerontic siphuncular segments are unknown, it is not demonstrated that the biconvex outline is attained. Early ephebic segments are planoconvex. Other features of the conch are not only more similar to *Hebetoceras* than to the more generalized *Montyoceras* but indicate that still further advances have taken place. The section is specialized in being more strongly depressed, with the ventral surface nearly flat. The septum surpasses that of *Hebetoceras* in depth and has attained the deeply subconical form found elsewhere only in the Silurian *Choanoceras*. The sutures have developed dorsal and ventral lobes separated by lateral saddles, presenting a pattern not found elsewhere in the Mixochoanites. The evidence shows that *Ecdyceras* is clearly a specialization in itself, and one developed from *He-*

betoceras rather than the simpler *Montyoceras*.

In only one of the features of *Ecdyceras* is the development of *Choanoceras* foreshadowed—namely, in the development of deep subconical septa. In other respects *Choanoceras* does not resemble *Ecdyceras* or, for that matter, any of the Hebetoceratidae. The section is compressed rather than depressed. No siphunuculear stages repeating the planoconvex segments so prevalent in the Hebetoceratinae are known.

Other features, however, indicate a relationship between *Choanoceras* and the Hebetoceratinae. First, the shells are slender and cyrtoconic. Only in *Ecdyceras* is the subconical septum of *Choanoceras* attained. The siphuncle of *Choanoceras* lies slightly ventrad of the center. The septa curve more sharply on the venter than on the dorsum, though they extend farther orad dorsally and produce sloping but unlobed sutures after the manner of the Hebetoceratinae.

In the course of the septa and the closure of the apex of the siphuncle at the septum of truncation, *Choanoceras* shows specialized features that can be traced back to the Hebetoceratinae. The septa of *Choanoceras* have become less evenly curved and more angulate in vertical section. The septum is nearly flat dorsally but bends abruptly as the siphuncle is approached. Gerontically, the dorsal septum is recurved instead of straight (text fig. 20). On the venter the septa become more and more sharply bent orad ventrad of the siphuncle. In the latest known stages the bend becomes so exaggerated that the adjacent septa fuse, simulating somewhat the fused septa of the ascoceroids. However, in *Choanoceras* fusion of the septa takes place on the ventral side of the shell, whereas in the ascoceroids such a phenomenon is strictly dorsal.

The closure of the septal foramen is produced partly by the deposits arising from the septal necks. Such deposits are not confined to a septum of truncation but occur in several successive camerae. They have the aspect of rather irregular annulosiphonate deposits. At the septum of truncation there is a small subconical plug, which closes the septal foramen, already made considerably smaller by the annulosiphonate deposits. Quite probably the conical plug is the homologue of the lens-shaped plate found in *Hebetoceras* and *Montyoceras*.

From the data reviewed above, it is evident that *Ecdyceras* and *Choanoceras* are derivatives of the Hebetoceratinae, in which the septa have become increasingly curved. Each, however, has developed its own specializations, and the present evidence does not indicate that the relationship between the two genera is particularly close. *Ecdyceras* is specialized in the depressed section and sinuate sutures. *Choanoceras* in the compressed section, specialized apical plate, and fusion of the adoral septa. It remains generalized, however, in the very gradual expansion of the siphuncular segments. In the earliest-known stage of the genus the segments are rather abruptly expanded, with the connecting ring adnate, and the brim apparently recumbent. The segments become abruptly though not greatly expanded at the time of appearance of the fused gerontic septa.

Lindström (1890) saw a possible connection between *Choanoceras* and a small unnamed orthochoanitic or suborthochoanitic form with conical septa. From his descriptions and illustrations (1890, p. 35, pl. 7, figs. 18–20) the siphuncle is central, a feature which would seem to eliminate this from the Mixochoanites. Its affinities are unknown. A somewhat similar form has been described by Foerste as *Orthoceras attawapiskatense* (1936, p. 262, text fig. 3), from the Attawapiskat limestone of Hudson Bay, as the name shouts rather than implies.

MORPHOLOGY AND EVOLUTIONARY TRENDS

Form.—The three oldest genera of the Mixochoanites, those described below from the Chazyan, consisting of slender naturally truncated conchs, shows that the group was derived from longiconic forms. These genera further serve to supply a connection between *Choanoceras* and other Mixochoanitic forms. In Middle Ordovician time the adoral end of the conch, consisting of the mature living chamber and a variable but small number of retained camerae, began to become inflated, as shown by *Probillingsites* and *Shamattawaceras*. Subsequent development of the ascoceroid septum produced *Schuchertoceras* in the Upper Ordovician

with no particular change in the form of the conch. Throughout these Ordovician genera the conch is gibbous, depressed in section, with an aperture extended only slightly beyond the gibbous portion, if at all. Subsequent modifications of form have to do with the development of a compressed section, seen first in *Lindstroemoceras*, elongation of the inflated part of the conch, and production of the aperture. Apparently a hyponomic sinus developed at the latest stage of the aperture; certainly the transverse markings of *Aphragmites*, *Ascoceras* and *Lindstroemoceras* show no trace of such a structure in slightly earlier stages of growth. Further, Lindström's illustrations show that if any sinus was developed over the early longiconic portion of the shell it was only vestigial. Evidence of the presence or absence of the structure in the Probillingsitinae is lacking. However, in *Montyoceras*, *Ecdyceras* and probably also in *Hebetoceras*, the sinus is quite well developed. Apparently it is true of this group, as of the Pseudorthoceratidae (Flower, 1939), that the hyponomic sinus is highly variable in its occurrence and is probably not of primary genetic significance.

In the elongation of the shell, extension of the aperture, and development of a compressed section, it is possible to see adaptive modifications. Compression is to be expected in a motile form, particularly when the center of buoyancy is well up on the dorsal side. This condition may be considered a mechanical modification following upon the development of the ascoceroid septa, for these result in the localization of the buoyant gas dorsad of the tissues of the living animal.

Again, the compressed form and the elongation of the shell produce the most perfect approach to the ideal stream-line form found in the cephalopods. The animal moves in a reverse direction, being propelled by the force of the hyponome. As a consequence the oblique septum of truncation, together with the shell wall, forms an excellent blunt nose, beyond which the shell soon attains its maximum diameter. Then, by reason of the produced aperture, the shell tapers more gradually to its termination. The outline is completed by the addition of the soft parts, consisting of a protruding head equipped with long tentacles. Doubtless the tentacles themselves, whatever their form and number, took on the function of rudders.

The condition of the aperture of the higher ascoceroids suggests reduction and specialization of the arms. It is doubtful whether the head was protruded far beyond the eyes, which would be essential in a motile organism, and which seem to be especially provided for in some forms by the development of dorsolateral sinuses in the aperture. Likewise the hyponome was protruded, a condition essential for swimming, though all forms do not possess the hyponomic sinus. There is no real evidence concerning the nature or number of the arms. It should be pointed out, however that the arms of *Nautilis*, which are numerous and short, are evidently specialized in the localization of a retractile fold, as suggested also by Dean (1901). Consequently the condition found in *Nautilus* cannot be considered typical of the Nautiloidea as a whole and is of no use whatsoever as a basis for reconstruction in such an independently specialized group as the ascoceroids, whose arms were probably long, few in number (as suggested by the restricted aperture), and might even have had some such finlike developments as the membranes found in the dibranchiate genus *Vampyroteuthis*.

Truncation and attendant specializations.—The demonstration of natural truncation during the life of an extinct animal is difficult and perhaps never quite conclusive. Fortunately the Mixochoanites show structural modifications attendant upon truncation, which leave little reason to doubt that the apical part of the shell was normally lost during life. However, natural truncation was originally proposed on the basis of quantitative evidence alone. Such evidence, is certainly convincing when applied to the numerous ascoceroids of Gotland or when applied to *Orthoceras truncatum* by Barrande, on the basis of a suite of over four hundred specimens. But quantitative evidence offers no solution in dealing with rare forms known from only a few specimens. Unfortunately this applies to most of the Ordovician forms, which, being old and possibly primitive, might not have been truncated as were the younger Silurian genera.

Truncation in *Hebetoceras*, *Ecdyceras* and *Montyoceras* is strongly suggested, but it is

not demonstrated conclusively by quantitative evidence. The small number of camerae found attached to living chambers suggests some such explanation, but the number of known specimens is quite small. Further, the locality that has yielded most of the known specimens shows abundant evidence of casual breakage of the cephalopod shells, not only after death but also following a preliminary burial during which the cavities within the shells were filled with inorganic materials.

Happily, two specimens show evidence of closure of the apex of the siphuncle by an elliptical mass of grey calcite, as seen in section (pl. 76, fig. 10), which contrasts sharply with the calcite filling the cavity of the siphuncle and also with the dove-colored limestone of the matrix. That no such plate has been found in many other forms, particularly those of the Middle and Upper Ordovician, may be attributed to conditions of preservation. Indeed, in most of these forms the siphuncle is incomplete and the entire extant portion of the conch is filled with sediment.

Lindström has reported and figured evidence of somewhat more complex apical plugs in the Silurian ascoceroids of Gotland. In *Ascoceras* proper Lindström illustrates the development of a structure closely resembling the collar of the Ammonoidea, which, from his figures, is actually a process of the septum, which bends anteriorly instead of posteriorly. Such structures have been found in the longiconic part of *Ascoceras manubrium* (Lindström 1890, pl. 3, figs. 17–18). Similar structures are known in the longiconic parts of other ascoceroids. At the base of the ascoceroid part of the conch of *Ascoceras*, *Glossoceras*, *Parascoceras* and *Pseudascoceras* similar processes, apparently springing from the septal neck, are visible. These require further study to demonstrate whether they are, as is suspected, specialized processes developed for holding a simple apical plate such as is found in the Chazy genera. There are some anomalous structures like that represented by Lindström for *Pseudascoceras* and reproduced here in text figure 10. Probably the anomalous situation is due in part to a section that does not quite attain the septal foramen but only cuts its margin.

Possibilities of natural truncation other than that due to accidental breakage are limited in nautiloids, particularly in orthoceracones, because of the extensive development of living tissue within the camerae, which has been discussed in some detail by the writer (Flower 1939, pp. 49–63). It is probably significant that the Mixochoanites are derived from a stock of cephalopods showing no development whatsoever of cameral deposits. This is true not only of *Sactorthoceras* Kobayashi and *Centroonoceras* Kobayashi but also of most of the cyrtochoanitic groups, which by their ontogeny can be traced to an origin in these suborthochoanitic forms, including the Oncoceratidae, Tripteroceratidae, and at least the Diestoceratidae of the actinosiphonate cephalopods.

Natural truncation in gastropods requires first that two things must happen: the soft parts must withdraw from the part of the shell to be removed, and some sort of partition must be built at the end of the portion to be retained. Subsequent to the withdrawal of the tissue the shell becomes brittle and is generally removed by abrasion. A casual inspection of gastropods will show also that the development of partitions closing off the apex normally precedes the destruction of the apical end. Indeed, in some forms several such partitions can be observed on one individual (Woodward, 1875, p. 36).

The problem of both withdrawal and the development of partitions is simpler in the cephalopods. The siphonal tissue is not bulky, and cameral tissue, if present, is evidently vestigial, judging from its failure to secrete any cameral deposits in the suborthochoanitic group. Atrophy of such tissue is a simple matter in contrast with the withdrawal of more extensive tissues of gastropods from the apex of the shell. Likewise, the septa serve as excellent partitions already in place, and the closure of the apex of the shell requires only the secretion of material by the apical end of the siphuncle, an organ capable of building much more elaborate structures, as is well evinced by many straight-shelled cephalopods.

Form of septa.—It seems to be generally considered, though the matter does not seem to have reached discussion in print, that the

primitive septum represents a segment of a sphere. The siphuncle is central, at the point of greatest depth, and the septa curve uniformly and symmetrically orad to the straight transverse suture. There is no reason why such a type should be primitive. Such a septum gives a superficial aspect of radial symmetry to an orthoceracone, but the cephalopod shell is fundamentally bilateral. Nevertheless, the type is certainly a simple one, though not necessarily primitive, and is found in *Sactorthoceras* the most generalized of the suborthochoanitic cephalopods. Curvature of the septum is little modified in *Centroonoceras*, though the siphuncle tends to lie somewhat ventrad of the center. In *Montyoceras* a marked advance is seen. The siphuncle here lies well ventrad of the center of the shell. The septum is curved asymmetrically in vertical section, being most strongly arched on the ventral side, and the sutures become oblique, sloping orad from venter to dorsum.

In *Hebetoceras* the same trend is carried further. Here the asymmetrical condition of the septum is more marked, largely by virtue of its much greater depth. However, shallower and more uniformly curved septa are regained in the gerontic stage. Septa modified in curvature are a new feature, though the modifications are not yet significant.

The vertically asymmetrical septum is a feature retained in the longiconic part of all later ascoceroids. It is retained also in the septum of truncation, where obliquity becomes much greater and the surface of the septum blends with the exterior of the shell to such an extent that the angular contact of septum and shell wall at the suture is practically eliminated.

In *Probillingsites* and *Shamattawaceras* the gerontic septa depart from the pattern shown in the earlier part of the conch, but instead of becoming shallow as in *Hebetoceras*, they become increasingly oblique, sloping orad from venter to dorsum. The extent to which this development is carried varies among the species, but never progresses to a point at which the dorsal saddle of the suture becomes separated in outline from the ventral portion. Such a development is the essential feature of the ascoceroid septum, together with fusion of the septa dorsal of the siphuncle and a tendency for the adoral septa to be discrete only dorsally and ventrally.

In the ascoceroids the removal of the apical part of the shell is localized at the septum of truncation, which, except for its tendency to blend with the shell surface to perfect the stream-line form of the organism, is a normal septum such as is found in *Hebetoceras*. In the simpler ascoceroids a second similar septum lies between this one and the first ascoceroid septum. This has been termed the basal septum.

Form of siphuncular segments.—Aside from the generalized suborthochoanitic segment found in longiconic ancestral types and possibly retained in the earlier part of the longiconic portion of more specialized forms, three distinct types of siphuncular segments occur in the Mixochoanites. Special terms are being proposed for these segments for the sake of brevity.

The planoconvex segment (text fig. 7) is straight on the dorsal or antisiphonal side of the conch, with septal neck and connecting ring parallel to the axis of the conch. It occurs throughout in *Montyoceras*, in the earlier segments of *Hebetoceras* and *Ecdyceras*, and is retained in the first prebasal segment of *Schuchertoceras iowaense*. Also, it apparently reappears in the first segment of *Pseudascoceras*, where, however, its phyletic significance might be questioned as was noted above. Further, it appears to be the prevailing form of the siphuncle in the longiconic portion of ascoceroids.

The *biconvex segment* (text fig. 8) is convex in outline on both dorsum and venter but is still essentially suborthochoanitic, with the septal necks scarcely recurved. It appears first in the gerontic stage of *Hebetoceras*. It appears in the ascoceroids wherever siphuncular segments connected with the basal septum are retained.

The *moniliform segment* (text fig. 9), is broadly expanded and markedly cyrtochoanitic. The septal neck is strongly recurved, generally recumbent, that is, turned back enough so that it comes into contact with the free part of the septum. The connecting ring lies in contact with the septa at either end. The segment thus formed is generally considerably broader and higher than long. Generally the first of the moniliform

segments is broader and longer than the others, but not nearly as high. These segments occur everywhere in conjunction with the ascoceroid septa, and, as such, are developed only in the Ascoceratidae as redefined below. Unfortunately there is no information concerning the later siphuncular segments of the Probillingsitinae, where something transitional between the biconvex and the moniliform segments might be expected.

Owing to the necessity of referring specifically to siphuncular segments intervening between the basal septum and the septum of truncation the term *prebasal segment* has been coined. Though the last of these properly belongs to the basal septum, the earlier ones do not and are actually relics of camerae whose septa have vanished. Consequently the use of such a simpler term as a "first basal segment" would be untrue in its implication.

Only in *Pseudascoceras* (text fig. 10) is there any serious deviation from the form types listed above. Here two segments intervene between the septum of truncation and the ascoceroid septum. The more adoral of these is apparently moniliform, except that it is not adnate adapically, and indeed does not contract at all upon approaching the relic foramen on the dorsal side. As a result the adapical segment, though somewhat broader than normal, is more nearly the planoconvex than the biconvex type. This is of particular interest in view of the fact that no such segment is retained in the mature individual in directly ancestral genera, namely *Lindstroemoceras* and *Parascoceras*, and indeed it is necessary to trace the line back to the generalized *Schuchertoceras iowaense* to find it in ascoceroids. Evidence is not conclusive concerning the interpretation of the structure here. It is possible that the planoconvex segment may again invade the mature shell, thereby crowding out the biconvex form so that there are only traces of some of its features in the second siphuncular segment. On the other hand, merely a simplification of siphuncular outline may be involved.

A unique feature shown in *Pseudascoceras decipiens* (Lindström) (text fig. 18) is a return to apparent larval conditions in the latest growth stage. The condition of the base of this genus has already been discussed above. The ascoceroid septa are accompanied by moniliform siphuncular segments. The first camera contains apparently two segments reminiscent of an ancestral condition in which a basal septum was developed. However, after the secretion of three ascoceroid septa which are fused closely dorsad of the siphuncle, four simple septa are secreted. The first apparently produces a biconvex segment, the other three secrete planoconvex segments. This was considered a case of rejuvenation by Miller (1932), although without discussion as to what he meant by the use of that term. Apparently it is a more fundamental procedure, the telescoping of an ontogenetic stage to a position other than that which it ordinarily occupies. As a result, the normal ontogenetic sequence of the ascoceroid is reversed, at least in regard to the succession of siphuncular outlines.

Reduction and ommission of ontogenetic stages.—(See text figs. 2–6). The loss of the septa and the siphuncular segments in the ontogenetic stages of the ascoceroids are so closely bound up with one another that they are best discussed together. The normal sequence seems to be a loss or resorbtion (it is not certain which) of the septa, leaving two or more siphuncular segments in a single cameral space, followed by the elimination of the more apical siphuncular segments.

It is to be expected on theoretical grounds that there should have existed a stage simpler than that shown by *Schuchertoceras iowaense*, one in which three septa were retained between the septum of truncation and the first ascoceroid septum. Such a hypothetical stage is shown in text figure 11. In *S. iowaense* only the most adoral of these septa is retained, but the siphuncular segments remain, of which the first is planoconvex, the two others biconvex. The transition from *S. iowaense* to *S. anticostiense* (text figs. 12, 13), shows the elimination of the first prebasal segment, while transition to *Lindstroemoceras* (text fig. 17), shows the reduction of the remaining free siphuncular segment. The next step is the elimination of the basal septum, leaving two siphuncular segments hanging in the space between the septum of truncation and the first ascoceroid septum. This is shown in *Pseudascoceras* (text fig. 18). The next step to be expected

from what has already been observed is the loss of the apical free siphuncular segment, a condition which is attained in *Ascoceras* (text fig. 19) and in the closely allied *Aphragmites* and *Glossoceras*.

As has already been mentioned, the scant evidence known suggests that *Billingsites* might be derived from *Schuchertoceras* by a similar reduction. It is perfectly possible that such hypothetical intermediate stages as are shown in figures 14 and 15 may be found when the interiors of more species have been studied. Certainly at the present time our knowledge of the internal structures of these genera is most inadequate, being based upon two species of *Schuchertoceras* and one of *Billingsites*, none of which are particularly well preserved internally.

The free siphuncular segments that occur at so many stages in the ascoceroids require study by thin section to determine the exact relationship between the connecting rings of successive free segments. It is evident that such outlines could not be maintained if the successive connecting rings were not long enough to come into contact with one another. Sections of many cephalopods of other groups have failed to show evidence of such continuity, as shown both by Teichert (1933) and Flower (1939).

Evidently the ascoceroids represent a remarkable case of lipopalingenesis, where the development is so speeded up that transitory ontogenetic stages are almost bodily removed, as it were, and it is possible to trace the removal step by step. What useful function this removal may have had is uncertain. Possibly it had to do with the shortening of the period of immaturity, a condition which is often advantageous, and in connection with which some amazing short cuts have been developed, as can be illustrated by the comparison of the embryology of a primitive insect with that of such a specialized form as the house fly. It is possible that, inasmuch as the ascoceroid could not attain effective motility until the mature conch was completed, that similar selective factors, at least, were at work on a series which was already tachygenetic.

CLASSIFICATION OF THE MIXOCHOANITES

It is evident that on the basis of the phylogenetic scheme presented above the families Schuchertoceratidae and Ascoceratidae cannot be regarded as distinct. Rather, they represent a single genetic line for which the older family name, Ascoceratidae Barrande should be retained. The family is here defined as including all ascoceroid conchs, that is, those possessing the typical ascoceroid septum, which is bent orad so abruptly on the dorsum as to make a sharp angle with the transverse portion of the septum, and further, these forms are divisible into two shell regions, a longiconic cyrtoconic portion, which is normally lost in the adult, and an inflated adoral portion.

Probillingsites and *Shamattawaceras* are clearly the ancestors of the group and are very closely related to each other; indeed, the differences so far demonstrated between the genera are not very fundamental and vary rather widely in species assigned to *Probillingsites*. It contrast to these gibbous forms of the Middle and Upper Ordovician, the Chazyan genera are slender. Both groups are here placed in the new family Hebetoceratidae, characterized as naturally truncated conchs of depressed section with the sutures asymmetrically curved vertically, the septa rising farther orad dorsally than ventrally, gerontic septa modified in curvature, gerontic siphuncular segments becoming increasingly expanded. Within this family it is convenient to designate two subfamilies, the Hebetoceratinae Flower, new subfamily, for slender conchs and the Probillingsitinae for conchs the mature portion of which is inflated.

The family Choanoceratidae Miller is retained for the Silurian genus *Choanoceras* and may be distinguished from the Hebetoceratidae by the gerontic fusion of septa ventrad of the siphuncle. The present distribution of genera and higher groups in the suborder Mixochoanites Hyatt, 1900, is as follows:

Family Hebetoceratidae Flower, n. fam.
- Subfamily Hebetoceratinae Flower, n. subf.
  - *Montyoceras* Flower, n. gen.
  - *Hebetoceras* Flower, n. gen.
  - *Ecdyceras* Flower, n. gen.
- Subfamily Probillingsitinae Flower, n. subf.
  - *Probillingsites* Foerste, 1928
  - *Shamattawaceras* Foerste and Savage, 1927

Family Ascoceratidae Barrande
- *Schuchertoceras* Miller, 1932

Billingsites Hyatt, 1884
Lindstroemoceras Miller, 1932
Parascoceras Miller, 1932
Pseudascoceras Miller, 1932
Ascoceras Barrande, 1847
Aphragmites Barrande, 1865
Glossoceras Barrande, 1865
Family Choanoceratidae Miller
Choanoceras Lindström, 1890

STATUS OF THE MIXOCHOANITES

The Mixochoanites were recognized as a suborder primarily on the basis of the abrupt change of the siphuncular outline from orthochoanitic, or, as delimited here, suborthochoanitic, to cyrtochoanitic. This, as has been shown above, is a feature confined to the more specialized members of the group. The youngest and most specialized forms, those of the Silurian, were the first ones known, and it is not surprising in view of the omission of phyletic stages in the ontogeny that they seemed so widely separated from other nautiloids as to deserve rank as a distinct subfamily. Subsequent study of the Middle and Upper Ordovician members of the group gave some indication of the gradual changes in ontogeny which approximate the phylogeny more closely, but material was too rare and usually too poorly preserved to show more than the relatively primitive nature of these forms. The Lower Ordovician material, however, serves to show even more primitive features and to shorten the gap between the Mixochoanites and other cephalopods to such an extent that the validity of the group as a suborder might be seriously questioned. However, it is pointless to enter upon a discussion of whether this suborder should be recognized at the present time, since the other and larger suborders will either have to be drastically revised or replaced by other groups. In view of the fact that the names of the present suborders fail in their original purpose of being descriptive, and the Suborder Cyrtochoanites at least is composed of isomorphic unrelated elements, complete replacement of the terms seems the preferable course. Quite possibly the Mixochoanites, as now delimited, constitute the only of Hyatt's original suborders that represents a closely knit genetic group.

It is now evident that the group characters which at first seemed to separate the Mixochoanites so widely from other cephalopods are all gradational in their development. Consequently the drawing of boundaries is a somewhat arbitrary matter. It would be strictly in accordance with the original concept of the group to delimit it to forms in which the siphuncle changes from orthochoanitic to cyrtochoanitic. This would include *Hebetoceras* and all higher forms but would exclude *Montyoceras*. The two genera are so closely related that it seems highly inadvisable to place them in different families, to say nothing of suborders. The form of the conch cannot be used without excluding not only the *Hebetoceratinae* but also the genus *Choanoceras*, a procedure of doubtful desirability.

The inception of natural truncation of the shell seems the best point at which to draw the line between forms that should properly be placed in the Mixochoanites and those that should be regarded as ancestral. It is a useful character, because there can hardly be gradation between truncated and untruncated conchs, although some practical difficulties are involved. Further, from the above account of the development of the Mixochoanites, it can be seen that this is the point at which the greatest structural break occurs, which is marked not only by shell truncation but also by the development of the peculiar vertical asymmetric curvature of the septum, which is a constant feature even in the longiconic portion of the latest and most specialized ascoceroids, and by the tendency for the gerontic septa and sutures to depart from the pattern maintained throughout the earlier part of the conch.

SYSTEMATIC DESCRIPTIONS

Order NAUTILOIDEA Zittel
Suborder MIXOCHOANITES Hyatt, 1900
Family HEBETOCERATIDAE Flower, n. fam.
Subfamily HEBETOCERATINAE Flower, n. subf.

Genus MONTYOCERAS Flower, n. gen.

Genotype: *Montyoceras arcuatum* Flower, n. sp.

Conch slender, cyrtoconic, exogastric, depressed in section, with dorsum and venter about equally rounded. The sutures are straight and slope apicad from dorsum to venter. Septa with the ventral portion more strongly curved than the dorsal portion.

Siphuncle less than half the distance from the ventral wall to the center of the conch. Its segments are suborthochoanitic, with the dorsal wall straight, the ventral and lateral outlines somewhat expanded. Living chamber slender, aperture with a shallow hyponomic sinus. In mature individuals the living chamber expands more gradually than does the earlier part of the conch.

Gerontically the septa become more closely spaced, less strongly curved. There is no gerontic increase in the expansion of the siphuncle, though the width becomes greater in proportion to the length of the segment, owing to the decrease in length which is the natural result of shortened camerae.

Natural truncation of the apex of the shell is a constant feature in the genus. All of the species known, including forms too fragmentary to merit description, are known from living chambers to which are attached, at the most, six camerae. The quantitative evidence, which is convincing but not conclusive, is supported by structural evidence, which shows the apex of the siphuncle to be closed by a lens-shaped plate.

Discussion.—*Montyoceras* is represented in our collection by about 30 individuals, which show considerable variation in size, section, curvature of the ephegic septa, curvature of the shell, and position of the siphuncle. Though it is evident that more species are involved than the few described below, our material is too fragmentary to warrant description of additional species at the present time. Further, these calcite-filled specimens do not separate readily from the matrix, and the preparation of adequate photographic illustrations is not possible for the majority of the specimens.

Ruedemann (1906, p. 497–499, pl 35, figs. 7–10) described *Ooceras lativentrum* from the Valcour limestone of Isle La Motte and Valcour Island. The specimens illustrated on his plate represent typical *Montyoceras*. Two specimens are illustrated, both of which, by the slight curvature of the septa, represent mature individuals. The type of plate 35, figures 7–9 is here selected as the holotype of *Montyoceras lativentrum* (Ruedemann). It is not certain whether the other specimen represents a new species or whether it represents *Montyoceras arcuatum*. The illustration represents an individual of the general size of *M. arcuatum*, but the living chamber is more slender and also more strongly curved. A third specimen figured as *lativentrum* (p. 498, text fig. 52) is neither conspecific nor congeneric with the other two. It represents a very different genus, being a longiconic actinosiphonate form representing a new genus, for which a new name is proposed in the writer's study of the Chazy Nautiloidea, still in manuscript.

Montyoceras is distinguished from the genus *Hebetoceras* and indeed all other Mixochoanites, by the failure of the gerontic siphuncular segments to expand. In *Hebetoceras* the siphuncular segments become widened in the gerontic camerae and their dorsal outline becomes convex. *Montyoceras* retains the planoconvex suborthochoanitic

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EXPLANATION OF PLATE 76

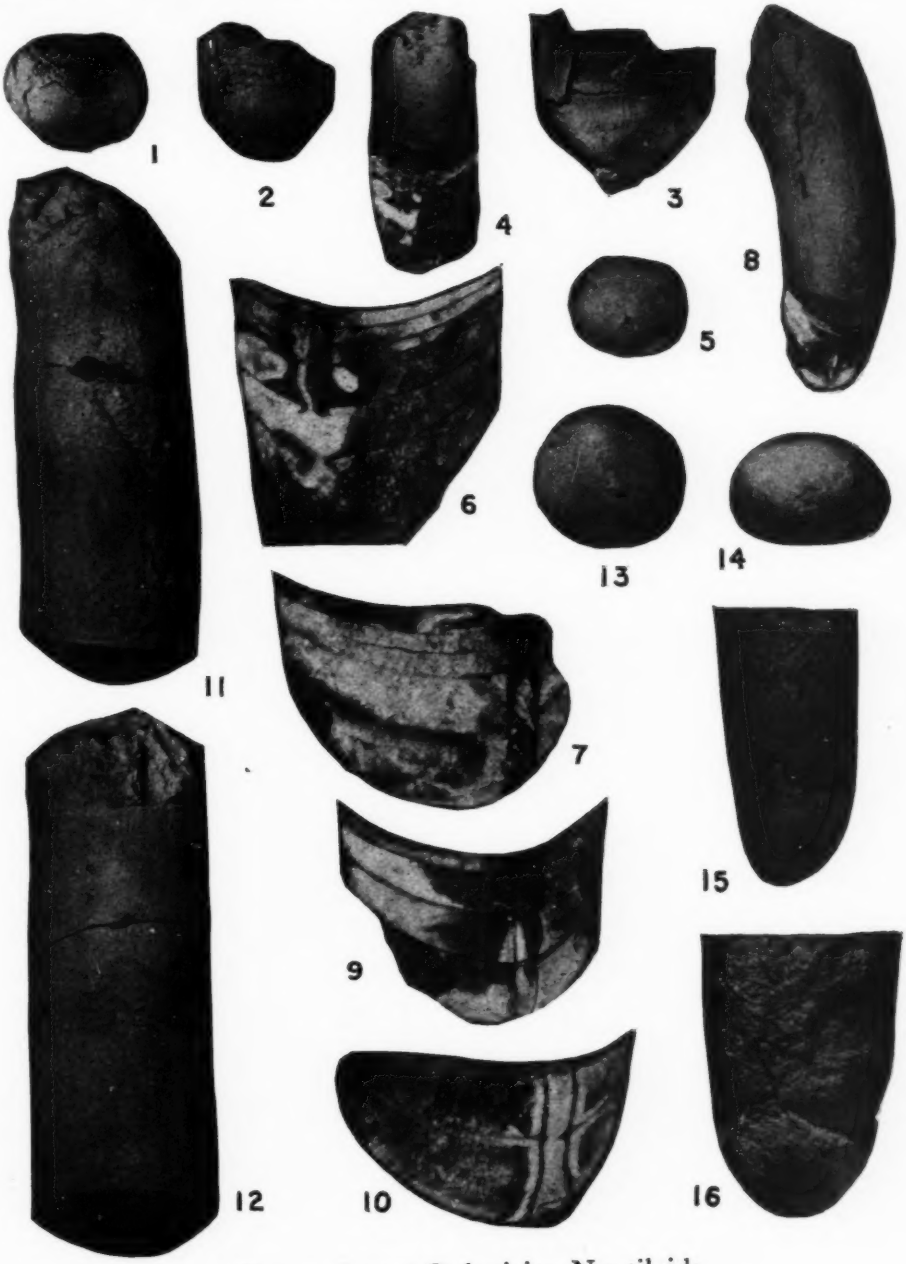
FIGS. *1–7*—*Hebetoceras mirandum* Flower, n. sp. *1*, Apical end of paratype, ×1, showing radial markings on septum. Paleont. Research. Inst. 5934. *2*, Paratype, ventral aspect, showing paired furrows on venter, ×1. Paleont. Research Inst. 5935. *3*, Ventral view of same specimen as *1*, showing conchial furrow, ×2. *4*, Holotype, lateral aspect, ×1, Paleont. Research Inst. 5932. *5*, Septum at base of living chamber of holotype, ×1. *6* Phragmocone of holotype, vertical section, venter on left, ×2½. Retouched to show septa and siphuncular outline. *7*, Vertical section of paratype, ×2½, on which adoral segments are not preserved, but apical end is complete. Paleont. Research Inst. 5933. Valcour limestone, Lower Ordovician, Little Monty Bay, Clinton County, New York. (p. 545)

8, *9*—*Montyoceras arcuatu* Flower, n. sp. Holotype, Paleont. Research Inst. 5931. *8*, Lateral view, ×1, venter on right. *9*, Phragmocone of same, ×2½, section vertical, showing simplicity of siphuncular segments in last camerae. Same locality. (p. 544)

10—*Montyoceras curviseptatum* Flower, n. sp. Sectioned surface of holotype, ×2½ showing apical plate closing siphuncle. Paleont. Research Inst. 5942. Same locality. (p. 544)

11–13—*Hebetoceras? cylindriforme* Flower, n. sp. Holotype, ×1. *11*, Left lateral; *12*, dorsal; and *13*, septal views. Paleont. Research Inst. 5938. Same locality. (p. 546)

14–16—*Ecdyceras sinuiferum* Flower, n. sp. Paratype, ×1, apical portion only, ×1; *14*, septal; *15*, left lateral; and *16*, dorsal views. Paleont. Research Inst. 5940. Middle Chazy, Clinton County, New York. (p. 547)



Flower, Lower Ordovician Nautiloids

Flower, Lower Ordovician Nautiloids

segments throughout life. In this respect *Montyoceras* is not mixochoanitic in the original sense of the term. As has been discussed above, it is included in the Mixochoanites because of its close relationship to *Hebetoceras*, which is such that the two genera cannot be placed in different families or higher groups. Other differences are of a purely secondary nature. *Hebetoceras* as now known consists of straight rather than arcuate species. There is reason to believe that the entire phragmocone, if retained, would show slight curvature. Further, one mature *Montyoceras* is known, though not described here, which appears to be either straight or very nearly so. There are normally more gerontic camerae in *Hebetoceras* than in *Montyoceras*, and the last septa of *Hebetoceras* are more markedly flattened than in *Montyoceras*. Both of these differences however are again features that possibly intergrade between the genera.

Montyoceras is distinguished from longiconic cyrtoceracones by the natural truncation of the apex of the phragmocone. Unfortunately this feature, fundamental though it appears to be, is one that it is often difficult to use owing to the fragmentary nature of many specimens representing actual longiconic forms. It is not at all uncommon to find living chambers to which only a few camerae are attached. In such circumstances natural truncation can be demonstrated conclusively only by the demonstration of the apical plate. Rather strangely, however, there are few longiconic cyrtoconic genera that are very similar to *Montyoceras*, even when accidental breakage simulates natural moulting of the apex of the shell. *Manitoulinoceras* Foerste (1924, p. 230) contains cyrtocones of depressed section in which the sutures slope orad on the venter instead of on the dorsum. *Clinoceras* Maeske (see Foerste, 1926, p. 34, pl. 31, fig. 2) is the only known longiconic genus that agrees with *Montyoceras* in the planoconvex siphuncular segments and also in having the peculiar vertical curvature of the septa seen again in the longiconic parts of the ascoceroids proper. Closer scrutiny shows however that *Clinoceras* has some specializations of its own. The side of the siphuncle closest to the wall of the conch and that assumed by Foerste to be ventral, is straight while the opposite side is expanded within the camerae. This is the reverse of the condition found in *Montyoceras* and *Hebetoceras*, where the orientation is based upon the hyponomic sinus and the furrows of the interior of the shell. Therefore it may be suggested that the orientation of *Clinoceras* has been wrong, and that the siphuncle actually lies dorsad of the center. If so, the curvature of the conch is exogastric rather than endogastric. *Clinoceras* departs further from the cyrtoconic pattern in having curvature confined to the apical part of the shell. Adorally the conch is straight. The shell bears a prominent constriction a short distance behind the mature aperture. Although orthoceracones commonly bear a similar constriction that is purely internal and due to the addition of material to the inside of the shell wall, the structure is quite different here, for the shell is constricted externally as well as internally.

Clinoceras is confined to the Ordovician of Europe. Its place in America seems to be taken by a somewhat similar form, *Whitfieldoceras* Foerste, in which the constriction of the living chamber is even more marked. The siphuncle of this genus has not been studied closely, but appears to consist of segments that are considerably more expanded than those of either *Montyoceras* or *Hebetoceras*.

Among other possible relatives of the ancestral stock that produced *Montyoceras*, there are several Ordovician genera of depressed cyrtoceracones including *Romingeroceras* Foerste, *Staufferoceras* Foerste, and the breviconic *Schofieldoceras* Foerste. Unfortunately the internal structure of these

EXPLANATION OF PLATE 77

FIGS. *1–3*—*Ecdyceras sinuiferum* Flower, n. sp. *1*, Paratype, ventral surface, Paleont. Research Inst. 5940. *2*, Left lateral and *3*, ventral views of holotype, a mature living chamber. Paleont. Research Inst. 5939. Slightly less than ×1. Middle Chazy limestone, Clinton County, New York. (p. 547)

4–5—*Montyoceras titaniforme* Flower, n. sp. Holotype, slightly less than ×½. *4*, right lateral; and *5*, ventral views. Paleont. Research Inst. 5941. Valcour limestone, Lower Ordovician, Little Monty Bay, Clinton County, N. Y. (p. 544)

genera is not known sufficiently well to permit accurate comparison. In form none of them approximate *Montyoceras* very closely.

Montyoceras is known only from the Valcour limestone of the Chazy, Lower Ordovician.

MONTYOCERAS ARCUATUM Flower, n. sp.
Plate 76, figures 8, 9

Living chamber with a ventral length of 40 mm., expanding from 15 mm. and 17 mm. to 17 mm. and 18 mm., with radius of curvature of venter of about 50 mm. Only the lateral part of the aperture is preserved on the holotype.

Phragmocone known from four camerae. The two apical camerae are 3 mm. in length each, the adoral two together measure 2½ mm. Siphuncular segments slender, suborthochoanitic, planoconvex in outline throughout. The siphuncle is 15 mm. in diameter at the septal foramen and 4 mm. from the venter throughout. The last segment is very slightly wider than the others as well as being much shorter. The depth of the septum is 3 mm. throughout, not materially modified gerontically. The plane of the suture is inclined about 18° from the normal transverse position.

Discussion.—The mature condition of the specimen is shown by the shortening of the last two camerae and also by a slight decrease in rate of expansion at the adoral end of the living chamber, which becomes slightly more depressed toward the aperture as well.

Type.—Holotype, Paleontological Research Institution no. 5931.

Occurrence.—Valcour limestone, Chazy, Lower Ordovician. From Little Monty Bay, southeast of Chazy village, Clinton County, New York.

MONTYOCERAS CURVISEPTATUM
Flower, n. sp.
Plate 76, figure 10

This species, based upon a fragmentary specimen is unique in combining a strongly curved form with very deep septa and also in having a siphuncle that is scarcely convex on the ventral side. Holotype 24 mm. in length, of which 17 mm. pertains to the phragmocone. Venter with radius of curvature of 100 mm. Basal septum with depth of 4 mm., at estimated diameters of 18 mm. and 19 mm. The angle of the suture is inclined about 22° with the transverse, taken normal to the ventral wall. The last two camerae contract rapidly; the first two camerae are 5 mm. and 4 mm. in depth, respectively; the third has a length of 4 mm., the fourth however measures only 0.8 mm.

Discussion.—Among several exceedingly fragmentary individuals this one stands out from all other representatives of the genus. The specimen is illustrated here largely because of the remarkably clear preservation of the apical lens-shaped plate, which closes the siphuncle in *Hebetoceras* and in *Montyoceras*.

Type.—Holotype, Paleontological Research Institution no. 5942.

Occurrence.—Valcour limestone, Little Monty Bay, southeast of Chazy, New York.

MONTYOCERAS TITANIFORME
Flower, n. sp.
Plate 77, figures 4, 5

The only representative of this species consists of the basal part of a living chamber and five adoral camerae. Conch expanding from 75 mm. and 60 mm. to 88 mm. and 60 mm. in a ventral length of 98 mm., and with a radius of curvature of about 200 mm. for the venter. The phragmocone has a ventral length of 35 mm., and a lateral length of 23 mm. The sutures are well exposed only laterally. The four adapical camerae are 5 mm. in depth, the last is 3 mm. in depth. A still shallower camera may lie orad of this, but the condition of preservation leaves the matter uncertain. Septum 10 mm. deep, curvature typical of the genus but considerably less arched than in other species. Siphuncle not clearly observed, evidently small and close to the ventral wall but not in contact with it, its structure not observed. The surface of the shell, though retained in part, is so overgrown and altered that none of the original features are preserved. The living chamber, with a ventral length of 70 mm., is obviously incomplete.

Discussion.—In form this species is typical of *Montyoceras*, It can be readily distinguished from other members of the genus by its gigantic size.

Type.—Holotype, Paleontological Research Institution no. 5941.

Occurrence.—From the Valcour limestone,

Chazyan, Lower Ordovician, at Little Monty Bay, southeast of Chazy village, Clinton County, New York.

Genus HEBETOCERAS Flower, n. gen.

Genotype: *Hebetoceras mirandum*, Flower, n. sp.

Conch slender, depressed in section, the known mature portion straight, though probably with the earlier stages slightly curved exogastrically. The mature individuals consist of at the most six camerae attached to the living chamber, the earlier portions of the phragmocone having been shed during life, and the open end of the siphuncle closed by the secretion of a small lens-shaped plate. The sutures are unlobed and slope slightly orad on the dorsum. The earlier septa are very strongly arched, the point of greatest depth lying well ventrad of the center, and the curvature being greater ventrally than dorsally. The gerontic septa are not only much more closely spaced but also become flattened, so that the curvature is greatly decreased. The siphuncle lies between the center of the conch and the ventral wall. The early segments are straight on the dorsum and faintly expanded on the venter. Such segments are found only in the early portion in connection with deep camerae and strongly arched septa. In the camerae which show the gerontic decrease in length the siphuncular segments become biconvex and then tend to widen by an increase in the distance between the walls as shown by the increased size of the septal foramen.

The living chamber of the holotype is incomplete. A hyponomic sinus is probably present as indicated by obscure lines of growth on the shell surface. A species referred to the genus with doubt shows in addition a broad shallow sinus on the dorsum.

Discussion.—*Hebetoceras* is closely allied to the preceding genus, *Montyoceras*, from which it differs in the straight form of the conch, the deeper ephebic camerae, and the more strongly and asymmetrically arched ephebic septa. The gerontic septa are more markedly shallowed than in *Montyoceras*, but the really essential advance shown in this genus is the development of biconvex siphuncular segments in the gerontic portion of the phragmocone.

Two species are referred to *Hebetoceras* below. The genotype is known from a half dozen specimens of mature phragmocones, but only one retains any considerable part of the living chamber. A second species, based upon a mature living chamber, is referred to the genus with doubt inasmuch as, in the absence of the phragmocone, the expansion of the later siphuncular segments can only be assumed on the basis of similarity of form with the genotype. Both of the species are from the Valcour limestone, Chazyan, of the Champlain valley.

HEBETOCERAS MIRANDUM Flower, n. sp.
Plate 76, figures 1–7

Mature individual small, a depressed orthoceracone with diameters at the base of the living chamber of 14 mm. and 16 mm. The living chamber is not completely known, the holotype possessing only the basal 17 mm. of the living chamber in a somewhat crushed condition. Phragmocone 6 mm. in length, measured along the wall, terminating in a subconical slightly convex septum of truncation, the septum of which is slightly oblique, sloping orad on the dorsum. The six camerae which make up the retained part of the phragmocone decrease in depth adorally, at the same time showing a decrease in the depth of the septa. The first septum is incompletely preserved; the second has a depth of 4 mm., the last a depth of 1 mm. The septal foramen is half again as large in the last septum as in the first two. The siphuncle is suborthochoanitic. On the dorsum the necks are short and straight; on the venter they are very faintly recurved, and the siphuncular outline is very faintly expanded. This condition holds in the three apical camerae retained in the mature individual. (Text fig. 2; pl. 1, figs. 5, 6.) The following three siphuncular segments are still suborthochoanitic in that the septal necks are not clearly recurved but are biconvex, and the diameter of the septal foramen increases toward the aperture.

Discussion.—The living chamber of this species, as in *Montyoceras*, was apparently very thin and only rarely preserved. Of the five specimens representing this species, only the holotype preserves any of the living chamber. The other specimens consist only of parts of the phragmocone of mature individuals.

The apical ends of the specimens present

some unusual features. The septal surface itself was apparently smooth but is not retained intact on any of the specimens. This is separated at its periphery by a distinct line from the wall of the conch. There is some indication of a structure closing the end of the siphuncle, but this is rarely well preserved and clear indication of its nature is found only in one individual. The internal mold of the septal surface retains a number of faint radial markings. On the midventral line appears a groove, stronger than the other markings, which seems to represent the conchial furrow—at least it corresponds to that furrow in position. However, the conchial furrow (Flower, 1939, p. 12) normally appears as a ridge on the internal mold instead of a groove. The present anomalous situation has not yet been explained, though it is not unique in the writer's experience. Subsequent to the discussion of the structure referred to above, similar grooves have been noted in two isolated instances, one on an undescribed brevicone from the Cherry Valley limestone, the other on the venter of *Protocameroceras brainerdi* (Whitfield) of the Fort Cassin limestone, Middle Canadian, of the Champlain valley.

One specimen consisting of two camerae represents an immature portion of this species. It is 6 mm. long as measured along the wall of the conch and has apical diameters of 6 mm. and 7 mm. The sutures are straight and scarcely inclined orad on the dorsum. The septum is 4 mm. in depth, and is deepest at the septal foramen, which lies 2 mm. from the venter. The adoral camera is filled with matrix and apparently was not closed anteriorly by a septum. This is the condition that might be expected in a part of the shell that had been naturally lost during the life of the organism. The structural and quantitative evidence of natural truncation indicate that it probably represents a fragment of a mature individual rather than an immature individual. It is remarkable chiefly in that it represents the only known example of an immature stage for this species, although it shows no features which were not already known from the other individuals.

Types.—Paleontological Research Institution. Holotype: no. 5932; paratypes: nos. 5933–5937.

Occurrence.—Valcour limestone, Upper Chazy, Lower Ordovician. All known specimens are from an outcrop half a mile west of Little Monty Bay, Lake Champlain, southeast of Chazy, Clinton County, New York.

HEBETOCERAS? CYLINDRIFORME
Flower, n. sp.
Plate 76, figures 11–13

The species is known only from a living chamber, depressed in section, which is slightly smaller at the aperture than at the base. Basal diameters are 22 mm. and 26 mm. In 60 mm. the aperture is attained with diameters of 22 mm. and 24 mm. The adoral third of the internal mold is constricted, probably indicating a thickening of the interior of the shell here. The internal mold is smooth. The basal suture is straight but markedly oblique, sloping orad on the dorsum or antisiphonal side. The septum has a depth of 4 mm. normal to the plane of the suture, and curvature is greater ventrally than dorsally. The septal foramen is 2 mm. in diameter and lies 8 mm. from the venter and 13 mm. from the dorsum. The aperture is imperfectly preserved but shows a broad sinus on the dorsum. Fragments of shell adhere to the mold but fail to retain surface features.

Discussion.—This living chamber is very suggestive of *Hebetoceras mirandum* in the straight form, depressed section, and in the condition of the sutures and the septum. The similarity is great enough to suggest strongly that this represents a species of *Hebetoceras* that differs from the genotype not only in its larger size but in the greater proportional distance of the siphuncle from the venter and the more oblique condition of the sutures. The generic reference cannot however, be regarded as conclusive in the absence of definite evidence of the gerontic development of biconvex siphuncular segments.

Type.—Holotype, Paleontological Research Institution no. 5938.

Occurrence.—Valcour limestone, Chazyan, Lower Ordovician, from Little Monty Bay, southeast of Chazy, New York.

Genus ECDYCERAS Flower, n. gen.

Genotype: *Ecdyceras sinuiferum* Flower, n. sp.

Conch orthoceraconic, expanding moderately in the early portion, becoming nearly

cylindrical in gerontic portion. Section strongly depressed, the venter flat, the dorsum arched, and the sides strongly curved. Septa very deep, suggesting *Choanoceras* Lindström, subconical in form, greatest depth attained well ventrad of the center of the conch. Sutures with ventral and dorsal lobes very strongly developed, the ventral lobe the deeper and narrower of the two. Siphuncle ventrad of the center of the conch, at point of greatest depth of septum. In ephebic camerae the siphuncular outline is suborthochoanitic and planoconvex as in *Montyoceras* and the earlier stages of *Hebetoceras*. Geronitc camerae are shortened without modification of the curvature of the septum. Gerontic siphuncular segments have not been observed. The surface bears coarse lines of growth, which show the presence of sinuses on both dorsum and venter.

Discussion.—The very deep septa give to this genus an appearance somewhat like that of *Choanoceras* Lindström, which differs in being curved, subcircular in section, and lacking any development of lobes and saddles. Internal differences are greater. *Ecdyceras* probably never extends farther in the modification of the siphuncular segment than the suborthochoanitic biconvex type found in *Hebetoceras* whereas in *Coanoceras* subspherical segments are attained. Further, *Ecdyceras* does not attain a fusion of gerontic septa, which is such a conspicuous feature of *Choanoceras*. Unfortunately the gerontic siphuncular segments have not been observed. The close similarity of this genus with *Hebetoceras* leads to the belief that such expanded segments were probably present here also. Indeed, one finds here several of the features in which *Hebetoceras* shows its advance beyond *Montyoceras* carried to even further extremes. The form has become straight rather than cyrtoconic. The early ephebic septa of *Hebetoceras* are becoming more strongly arched; in this respect *Hebetoceras* is intermediate between the other two genera. The same is true of the depressed condition of the conch. The sutures, however, show a development independent of that occurring in any other myxochoanitic forms.

A section of a hypotype shows clear indication of the presence of some structure closing the apex of the siphuncle, though its form is not clearly marked. This individual retains only two camerae. Its immature condition is shown by the relatively rapid expansion of the conch.

Ecdyceras resembles a gigantic *Allumettoceras* in external features and can be best distinguished by the natural truncation of the apex and the suborthochoanitic ephebic siphuncular segments, *Allumettoceras* is longiconic, and although the earliest siphuncular segments are suborthochoanitic they are not planoconvex, and they are confined to a much earlier part of the conch, being rapidly modified into subspherical cyrtochoanitic segments. Further, no known *Allumettoceras* attains half the size of *Ecdyceras*, a character which is useful though hardly of fundamental value.

Ecdyceras is as yet known only from the genotype, from the Middle Chazy of the Champlain valley.

ECDYCERAS SINUIFERUM Flower, n. sp.
Plate 76, figures 14–16;
plate 77, figures 1–3

Conch straight, depressed in section, the venter strongly flattened, the dorsum gently arched. Rate of expansion rapid in the early stages, increasing from 26 mm. and 18 mm. to 34 mm. and 22 mm. in a length of 80 mm. The mature living chamber however, becomes subtubular, expanding from 38 mm. and 25 mm. at its base to 44 mm. and 28 mm. at the adoral end in a length of 100 mm. The sutures have been discussed in the generic description. The deepest part of the septum lies twice as far from the dorsum as from the venter. Curvature is strongly asymmetrical in the vertical plane. The siphuncle lies well ventrad of the greatest depth of the septum in the early ephebic, portion, but is nearly terminal in the gerontic portion. On the holotype the septum has a maximum depth, measured from the lateral saddles of the suture, of 22 mm., where the dorsoventral diameter is 25 mm.

Only one siphuncular segment has been observed; this is found in an immature individual at conchial diameters of 16 mm. and 22 mm. The segment is 5 mm. in length, 1 mm. in diameter at the septal foramen, and 1 mm. from the venter. It is suborthochoanitic as in early ephebic *Hebetoceras*. The gerontic septa are closely spaced but fail to show the reduction of curvature found in

Hebetoceras. The gerontic siphuncular segments are unknown.

No aperture is preserved complete. The holotype shows by its coarse lines of growth the presence of a broad, conspicuous hyponomic sinus and a narrower and very slightly shallower sinus on the dorsum.

Discussion.—This species is known to me only from four specimens, all from the same locality. The limestone is black, slightly silicious, and not very favorable for the preservation of fine detail. The one sectioned individual shows at the apical end of the siphuncle a small mass of calcite, which may represent the apical plate that closes the siphuncle during life and subsequent to the truncation of the apical part of the shell. However, in the same section are several identical calcite masses that are entirely adventitious, and these suggest that the calcite in the siphuncle may be adventitious also. The septum, when well preserved, is smooth and shows none of the radial impressions noted in *Hebetoceras*. A peculiar feature of the species is the development of a basal zone on the ventral side of the mature living chamber, which follows the course of the suture.

Types.—Paleontological Research Institution. Holotype, no. 5939; paratype, no. 5940.

Occurrence.—All specimens are from a black silicious limestone containing abundant *Stromatocerium*, directly overlying the bed containing *Macleurites* in great numbers, with *Gonioceras chaziense* Ruedemann, *Michelinoceras modestum* (Ruedemann) and other cephalopods. This is found about 1 mile along the road from Chazy to West Chazy, in a field on the north side, where it forms conspicuous ledges. Crown Point limestone, Middle Chazyan, Lower Ordovician.

REFERENCES

BARRANDE, J., *1855*, Sur *Ascoceras*, prototype des nautilides: *Soc. geol. France, Bull.*, sér. 2, t. 12, pp. 157–177.

——, *1865–77*, *Système silurien du centre de la Bohême* pt 1, t. 2, *Cephalopodes*. Prague.

BILLINGS, E., *1865*, Paleozoic fossils, vol. 1, *Canada Geol. Survey*, pp. 17, 18, 163, 164.

DEAN, B., *1901*, Notes on living *Nautilus: Am. Naturalist*, vol. 35, pp. 819–837.

EICHWALD, E., *1860*, *Letheae Rossica ou Paleontologie de la Russie*, vol. 1, pt. 2. Stuttgart.

FLOWER, R. H., *1939*, Study of the Pseudorthocertidae: *Paleontographica Americana*, vol. 2, no. 10.

——, *1939a*, *Harrisoceras*, a new structural type of orthochoanitic nautiloid: *Jour. Paleontology*, vol. 13, pp. 473–480, pl. 49.

FOERSTE, A. F., *1924*, Upper Ordovician faunas of Ontario and Quebec: *Canada Geol. Surv. Mem.* 138.

——, *1926*, Actinosiphonate, trochoceroid and other cephalopods: *Dennison Univ., Sci. Lab., Bull.*, vol. 21, pp. 284–384, pls. 32–53.

——, *1928*, Cephalopoda, in Twenhofel, Geology of Anticosti: *Canada Geol. Survey, Mem.* 154, pp. 258–262.

——, *1928*, Some hitherto unfigured Ordovician cephalopods from Anticosti Island: *Royal Soc. Canada, Trans.*, ser. 3, vol. 22, pp. 223–225.

——, *1936*, Some new Silurian cephalopods and crinoids, chiefly from Ohio and Hudson Bay: *Ohio Jour. Sci.*, vol. 36, pp. 261–272, 2 pls.

HYATT, A., *1884*, Genera of fossil cephalopods: *Boston Soc. Nat. Hist., Proc.*, vol. 22, pp. 253–338.

——, *1898*, Phylogeny of an acquired characteristic: *Am. Philos. Soc., Proc.*, vol. 22, pp. 348–616, pls. 1–14.

——, *1900*, Cephalopoda, in Zittel-Eastmann *Textbook of Paleontology*, pp. 502–592. London and New York.

KOBAYASHI, T., *1934*, the Cambro-Ordovician formations and faunas of South Chosen, Paleontology, Part I, Middle Ordovician faunas: *Tokyo, Imp. Univ. Fac. Sci. Jour.*, sec. 2, vol. 3, pt. 8.

LINDSTRÖM, G., *1890*, The Ascoceratidae and Lituitidae of the Upper Silurian formations of Gotland: *K. svenska vetensk. akad. Handl.*, bind. 23, no. 12.

MILLER, A. K., *1932*, The mixochoanitic cephalopods: *Iowa Univ. Studies in Nat. History*, vol. 14, no. 4.

——, *1934*, A mixochoanitic cephalopod from Iowa: *Am. Jour. Sci.*, ser. 5, vol. 26, pp. 178–182.

RUEDEMANN, R., *1906*, Cephalopoda of the Champlain Basin: *New York State Mus., Bull.* 90, 611 pp., 38 pls.

ULRICH, E. O., and FOERSTE, A. F., *1933*, The earliest known cephalopods: *Science*, n. s., ser. vol. 78, pp. 288–289.

WOODWARD, S. P., *1875*, *A manual of the mollusca*, ed. 3, London.

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MESOGAULUS PRAECURSOR, A NEW RODENT FROM THE MIOCENE OF NEBRASKA

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ABSTRACT—A new species of mylagaulid rodent is described from the "Upper Harrison" beds of Nebraska. These beds are distinct from the overlying Marsland formation and contain a fauna more closely related to that of the Arikaree than to the Marsland fauna. The dentition of *Mesogaulus praecursor*, n. sp. is more primitive than that of other species of *Mesogaulus* but more advanced than that of *Mylagaulodon*. *Mesogaulus* is redefined and four species of "*Mylagaulus*" are referred to it.

THE SPECIMEN here described was collected by H. J. Cook on October 2, 1907, in the "Upper Harrison" beds of Nebraska. It has remained undescribed since that time because it was hoped that more complete material would be found. As better specimens have not been forthcoming, we are now describing these fragmentary remains. They belong to a primitive member of the Mylagaulidae structurally intermediate between the older *Mylagaulodon angulatus* Sinclair from the upper part of the John Day formation and the next younger species, which occur in the middle Miocene Sheep Creek beds.

The beds in which the specimen of *Mesogaulus praecursor* was found have long been known as the Upper Harrison formation. (Peterson, 1906, pp. 21–24) Recent discussion has led to a certain amount of confusion concerning the terminology of these beds. Cook pointed out (1915, pp. 71–72) the existence of an angular unconformity between the typical Harrison formation ("Lower Harrison") and the so-called "Upper Harrison" beds. The latter are not the upper part of the Harrison formation as originally defined by Hatcher (1902, p. 117), but a separate, later formation, with characteristic lithology and fossils. Recently Schultz attempted to rectify this undesirable nomenclature by introducing the name Marsland formation (1938, p. 443) for

> the deposits ("Upper Harrison beds") which immediately overlie the Arikaree group and which are faunally and lithologically distinct from the typical Arikaree.[1]

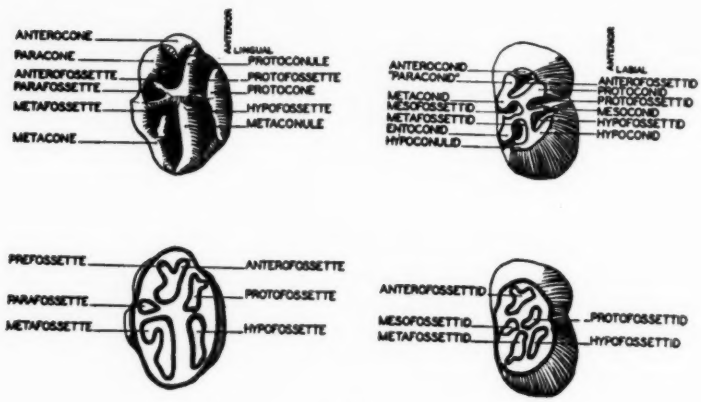
[1] He redefines Arikaree as a group name to include the Gering, Monroe Creek, and Harrison formations. See also Lugn, 1939, pp. 1251–1254.

Schultz adds that

> This formation is best exposed in Nebraska in the region about Marsland along the Niobrara River, where it includes some 150 feet of buff and gray, soft sandstone.

However, these beds near Marsland, from which the University of Nebraska has obtained a rich and as yet undescribed fauna, are not the "Upper Harrison" beds, but later and distinct from them. The Marsland formation as defined by Schultz includes therefore two separable formations, the "Upper Harrison" beds and the higher, previously unnamed deposits exposed east of Marsland. Because of the faunal distinctness of the beds around Marsland from the "Upper Harrison," it seems desirable to restrict the use of the term Marsland formation to the deposits at the type locality described by Schultz. The restricted Marsland formation is equivalent to the "unnamed beds" between the "Upper Harrison" and Sheep Creek, shown in the columnar section of the region by Cook and Cook (1933, p. 44). The Marsland fauna is intermediate between those of the "Upper Harrison" and Sheep Creek. It is characterized by *Aletomeryx* and especially by the first appearance of *Merychippus*, which is absent from the "Upper Harrison" fauna.

Until the earliest deposits of the Hemingford group, which lie below the restricted Marsland formation, are adequately described, we shall refrain from proposing a name for them but continue to refer to them as the "Upper Harrison" formation in spite of the acknowledged undesirability of that name. Although the "Upper Harrison" beds are included within the Hemingford group



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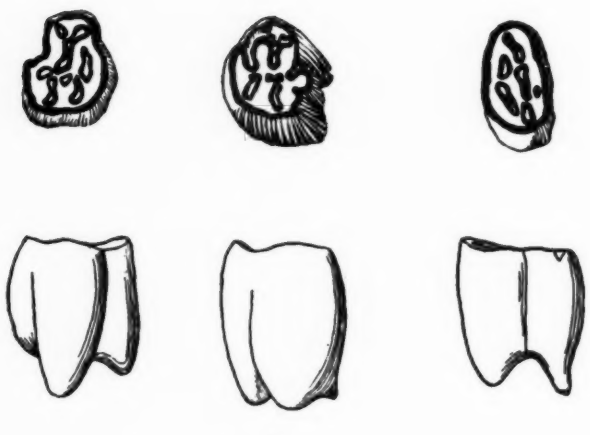

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FIGS. *1*—Terminology of mylagaulid teeth, based on *Mesogaulus vetus* Matthew, approximately ×2. Left: upper fourth premolar, right: lower fourth premolar. The term "paraconid" is used purely as a topographic designation for want of an adequate substitute and in no sense implies homology with the paraconid of normal tritubercular teeth. In *Mylagaulus laevis* and later species a parafossettid occurs in the lower premolars between the anterofossettid and mesofossettid.

2—*Mesogaulus praecursor* Cook and Gregory, n. sp. Type specimen, HC. 137, ×2. Occlusal and medial views. Left: right P^4. Center: left P^4. Right: left P_4.

of Lugn (1938, p. 226; 1939, p. 1253), their fauna is of Arikareean, or lower Miocene aspect. The first appearance of *Merychippus* is the most suitable paleontological guide to the middle Miocene (Hemingfordian) in North America, and this genus does not occur in the "Upper Harrison." The local folding in western Nebraska which separates the Arikaree and Hemingford groups occurred in lower Miocene time and did not coincide with any marked faunal change (only specific differences).

Genus MESOGAULUS Riggs, 1899

RIGGS, E. S., *1899*, Field Columbia Mus. Pub., Geol. ser., vol. 1, p. 181.

Generic definition: Hornless Mylagaulidae in which the lower premolars have developed the protofossettid, hypofossettid, anterofossettid, mesofossettid, and metafossettid. Upper premolars with persistent Y-shaped anterofossette and relatively well developed columnar mesostyle. Skull broad and depressed, of typical mylagaulid form.

Mesogaulus differs from *Mylagaulodon* in the much greater hypsodonty and relatively larger size of the fourth premolars, in the closer approach of those teeth to the typical mylagaulid form by anteroposterior elongation and loss of the ridgelike character of the mesostyle, and in the greater relative breadth of the skull. It differs from *Mylagaulus* in the absence of a parafossettid at any stage in the wear of the lower premolar, in the smaller size and lower crowns of the premolars, and in the retention of a columnar mesostyle on P^4.

Generic range: Late Arikareean to Barstovian. (Late lower to upper Miocene.)

Genotype: *Mesogaulus ballensis* Riggs.

To *Mesogaulus* are referred: *M. pristinus* (Douglass), *M. proximus* (Douglass), *M. paniensis* (Matthew), *M. vetus* (Matthew), and *M. praecursor* Cook and Gregory, n. sp. The last is in many respects more primitive than the other species but scarcely different enough to deserve separate generic position.

MESOGAULUS PRAECURSOR Cook and Gregory, n. sp.

Type: Left and right P^4 and left P_4, collection of H. J. Cook, No. HC 137. Locality and horizon: Four miles north of Agate, Nebraska, 100 feet above base of Upper Harrison formation. Arikareean (Lower Miocene) age.

Diagnosis: Small species with much lower-crowned premolars than other mylagaulids except *M. angulatus*. Upper premolars more nearly quadrate than in later forms, rather narrow anteriorly, and distinctly broader posterior to the mesostyle. Parastyle well developed; protocone far posterior; prominent parastria; well-developed mesostylar pillar. Lower premolar long-oval in pattern, without parafossettid.

Description and comparisons: The teeth were found within three or four inches of one another, and probably belonged to a single individual. Fortunately they are worn only sufficiently to develop the pattern. The right upper premolar is somewhat more worn than the left, though it is not impossible that they belonged to the same individual. Most striking in comparison with later Tertiary species is the relatively low crown of these teeth; they are nevertheless distinctly hypsodont, and thus intermediate between the brachyodont *Mylagaulodon angulatus* of the John Day and the later forms. The breadth of the upper premolars in relation to their length recalls *Ceratogaulus rhinocerus*, from which they are readily distinguishable by their smaller size and more strongly developed mesostyle. The proportions of the crown are intermediate between those of the later mylagaulids and *M. angulatus;* they recall those of *Meniscomys hippodus* somewhat. Further resemblances to *Mylagaulodon* and *Meniscomys* may be found in the retention of the mesostyle and distinctly posterior position of the protocone. The mesostyle forms a distinct ridge on the outside of the tooth, and the parastria in front of it extends to the base of the crown. It is no longer riblike, as in the allomyids and *Mylagaulodon*, however. In the left premolar the mesostyle is a conspicuous fold separated from the metacone by a well-defined mesostria; the latter is very weak in the opposite tooth. Increase in breadth posterior to the mesostyle is accomplished mainly by development of the outer side of the tooth. The metacone lies almost directly behind the mesostyle, lateral to an anteroposterior line through the paracone. This lateral part of the tooth is supported by a third root, opposite that of the protocone; the anterior part of the crown rests upon a single root. The protocone is short compared to the entire anteroposterior length of the crown and is placed posterior to the middle of the tooth. Its form recalls that of *Mesiscomys*, but its position is more posterior than in that genus and similar to *Mylagaulodon*. The parastyle (or anterocone) seems better developed in these teeth than in some later species, recalling again the primitive allomyid condition. This condition is most noticeable on the right tooth.

Summarizing, the upper premolars of *M.*

praecursor appear intermediate between those of later mylagaulids and *M. angulatus* because of: (1) relatively low yet hypsodont crowns, (2) great breadth relative to length, (3) mesostyle well developed but not riblike, (4) posterior position of protocone, and (5) well-developed parastyle.

The lower premolar does not show any especially primitive characters, and aside from its smaller size and markedly lower crown it is not distinguishable from other species of *Mesogaulus*. The difference in size, combined with the lower crown, fits well with the evolutionary tendencies toward increase in size and hypsodonty of the premolars observed among mylagaulids of successive geologic ages. At present, comparisons cannot be made with the Sheep Creek *M. novellus*, which may be a somewhat smaller species.

Some undescribed premolars in the American Museum of Natural History, which may belong to *M. novellus*, differ markedly from *M. praecursor* in their higher crown and more slender proportions. These are the only known permanent mylagaulid teeth smaller than *M. praecursor* in length and breadth except the brachyodont *M. angulatus*.

The lower premolar of *M. praecursor* is distinctly shorter anteroposteriorly than that of *M. ballensis* and the allied *M. paniensis*, *M. vetus*, *M. pristinus*, etc., and the upper premolars are correspondingly shorter than the known upper teeth of those species. There are no satisfactory distinctions in the pattern of the lower molars to separate these species from the Upper Harrison form, but the relatively low crowned teeth of the latter at once show that it is distinctly more primitive.

Relationships: Although teeth of *Mesogaulus praecursor* are intermediate in most respects between those of *M. angulatus* and the various later mylagaulids, they present no special indications or relationship to any of the later species. The similarity of pattern to *Ceratogaulus rhinocerus* mentioned above is only in the retention of relatively primitive proportions by the latter and thus cannot be considered as indicative of affinity. The slender teeth of *M. novellus* may have been derived from an earlier stage than *M. praecursor*, but this is not certain. No known features of *M. praecursor* would bar it from direct ancestry to any of the other later forms.

Measurements in millimeters

	Length crown	Maximum length tooth	Width crown	Maximum width	Height
Lower pm	7.3	7.9	4.1	4.2	7
Left P^4	6.0	7.7	5.3	6.0	10.5
Right P^4	6.7	7.8	5.5	5.8	7.4

REFERENCES

COOK, H. J., *1915*, Notes on the geology of Sioux County and vicinity, Nebraska: *Nebraska Geol. Survey*, vol. 7, pp. 59–75, pl. 1, figs. 1–7.

COOK, H. J., and COOK, M. C., *1933*, Faunal list of the Tertiary Vertebrata of Nebraska and adjacent areas: *Nebraska Geol. Survey, Paper* No. 5, pp. 9–58.

DOUGLASS, EARL, *1903*, New vertebrates from the Montana Tertiary: *Carnegie Museum, Annals*, vol. 2, pp. 145–199, figs. 1–37, pl. 2.

HATCHER, J. B., *1902*, Origin of the Oligocene and Miocene deposits of the Great Plains: *Am. Philos. Soc., Proc.*, vol. 41, pp. 113–131.

LUGN, A. L., *1938*, The Nebraska State Geological Survey and the "Valentine problem": *Am. Jour. Sci.*, ser. 5, vol. 36, pp. 220–227.

——, *1939*, Classification of the Tertiary system in Nebraska: *Geol. Soc. America, Bull.*, vol. 50, pp. 1245–1276, 1 pl.

MATTHEW, W. D., *1902*, A horned rodent from the Colorado Miocene, with a revision of the mylagauli, beavers, and hares of the American Tertiary: *Am. Mus. Nat. History, Bull.*, vol. 16, pp. 291–310, figs. 1–17.

——, *1924*, Third contribution to the Snake Creek fauna: *idem*, vol. 50, pp. 59–210, figs. 1–63.

PETERSON, O. A., *1906*, The Miocene beds of western Nebraska and eastern Wyoming and their vertebrate faunae: *Carnegie Mus. Annals*, vol. 4, pp. 21–72.

RIGGS, E. S., *1899*, The Mylagaulidae, an extinct family of sciuromorph rodents: *Field Columbian Mus. Pub., Geol. Ser.*, vol. 1, pp. 182–187.

SINCLAIR, W. J., *1903*, *Mylagaulodon*, a new rodent from the upper John Day of Oregon: *Am. Jour. Sci.*, ser. 4, vol. 15, pp. 143–144, fig. 1.

SCHULTZ, C. B., *1938*, The Miocene of western Nebraska: *idem*, vol. 35, pp. 441–444.

MANUSCRIPT RECEIVED BY THE EDITOR MARCH 4, 1941.

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THE SOFT ANATOMY OF BOTHRIOLEPIS

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ABSTRACT—Sectioned specimens of the armored fish *Bothriolepis canadensis* from the Upper Devonian of Scaumenac Bay, Quebec, show the form and position of some of the soft organs preserved by differential filling with sediments. It is thought that only those organs are preserved which communicate with the exterior and thus could be filled with sediment prior to their decomposition. The alimentary tract is seen to be a relatively simple straight tube with an expansion in the posterior part of the trunk having a spiral structure comparable to the spiral valve of elasmobranchs. Gills are indicated and are restricted to the head region. From the pharynx arise two large paired ventral sacs, which extend posteriorly about one-third the length of the trunk. These are interpreted as lungs, a conclusion which seems plausible when we consider that *Bothriolepis* was a gnathostome and was living in close association with Dipnoi and Crossopterygii, both of which probably had developed lungs by the Upper Devonian. Paired structures protruding from the posterior end of the carapace have been interpreted by others as pelvic fins or frills but may have had a reproductive or excretory function.

THE COLLECTION of the late Professor William Patten, now in the Dartmouth College Museum, contains several hundred specimens of the armored fish *Bothriolepis canadensis* Whiteaves from the Upper Devonian of Scaumenac Bay, Quebec. Sectioned specimens show structures within the carapace which appear with such regularity of position and shape that there can be no doubt that they represent some internal organs of *Bothriolepis*. The preservation of their form is due to the fact that the organs are filled with sediments of different types from that surrounding the animal exteriorly and filling much of the interior of the carapace.

GEOLOGIC CONSIDERATIONS

Three different sediments may be recognized in sections of *Bothriolepis*. The most prominent is pale greenish-gray and has the appearance of a medium-textured sandstone. Thin sections show that it consists in considerable part of calcite through which are sprinkled numerous grains of ferromagnesian minerals and many very angular quartz fragments, which prove its clastic nature. This sediment fills much of the carapace and surrounds the animal on the exterior. The second sediment is similar in composition but is distinguished by its much finer texture. This is the filling which preserves the form of many of the organs. The third sediment is sharply distinct. It is a fine-grained siltstone containing angular quartz fragments, micas, ferromagnesian minerals, etc., but little or no calcite. It is invariably present as a flattened ellipsoidal structure in the trunk carapace and is interpreted as the filling of the intestine and rectum. It was found that staining with malachite green emphasized the contrast between these three sediments, the finer-grained parts taking the stain more readily than the coarser.

Since many of the interpretations in this study have their basis in the geologic processes and their results, it is necessary to review the evidence bearing on the habitat and mode of death of *Bothriolepis* at Scaumenac Bay. A small coal seam near the base of the Escuminac beds is evidence that deposition was continental at that time, while in the "fish beds" the abundance of land plants and the presence of Dipnoi, Crossopterygii, acanthodians and cephalaspids strongly suggest that continental conditions existed in the upper part of the section. In the disposition of the remains of *Bothriolepis* and in the orientation of the plants, there is evidence of current action. In fact, according to Patten (1912, p. 379), there is similar orientation of specimens of *Bothriolepis* at different levels. A constant current under continental conditions clearly indicates fluviatile conditions.

Patten obtained most of this material from a single small "table." The lenslike nature of the deposit suggests a channel or a pool in a floodplain, while the crowding of

ferns, *Bothriolepis*, and other fish in some beds might be considered to favor the latter hypothesis.

Evidence upon the manner of feeding of *Bothriolepis* is found in the fine muddy or silty stone usually present in the posterior alimentary tract. It indicates that this fish was a mud-grubber, living much as does an earthworm upon digestible material in the mud it swallows. As such it was a bottom feeder, as is indicated independently by the ventral position of its mouth. That plant food formed an important part of its diet is indicated by the frequent presence of carbonaceous material in the alimentary tract.

The cause and manner of death is of importance in explaining the differential filling of the body by sediments. It is obvious from the number of individuals at one level and in one small area that this cause was, from the point of view of *Bothriolepis*, of a catastrophic nature. Drying up of water holes is suggested as a possible hypothesis, but there are two important objections. First, the occasional preservation of the soft tail in an upright position would require that burial took place soon after death. Moreover, the filling of those organs which communicate with the exterior must have occurred before decomposition had gone far, and presumably could be accomplished better by water-borne than by wind-borne sediment. Secondly, the evidence that the fish and ferns were oriented directly or indirectly by current action would require the drought to be followed immediately by wet conditions at just the right time.

The possibility that foul or superheated waters were the cause of death is also rejected, since currents would make it unlikely that the waters would reach such a condition.

The most acceptable hypothesis is that the fish, living in pools, were overwhelmed by excessively muddy waters which were sufficiently turgid to clog up their respiratory apparatus or impede their respiration in some manner. The fine mud in the alimentary tract of *Bothriolepis* indicates that this was the type of sediment at the bottom of the presumed pools in which it lived. The sediment filling and burying the fish is of a considerably coarser texture, however. It could have been carried by swifter waters, presumably those of a stream in flood, which might have been highly charged with sediment. Such waters would account for the filling with sand of those organs which communicate with the exterior. The sediment filling these organs, or at least that which is now distinguishable, was of a finer texture than that which later buried the animal. The latter was perhaps carried by still higher waters of the same flood.

The sedimentary story might be summarized as follows: First, the alimentary tract was filled in normal feeding with the fine mud from the bottom of the pool. Then came flood waters highly charged with limy, sandy sediment of fine texture, which caused the death of the fish and filtered into those internal organs which had an open communication with the exterior. Finally, the animal was buried with coarser, limy sand and upon decomposition of the soft parts this material filled the remainder of the interior of the carapace.

THE SOFT ANATOMY

It is believed that there is preservation of the form of only those organs which could have been filled with sediment prior to their decomposition, namely, those which communicate with the exterior. The following systems fit this condition: alimentary, respiratory, urogenital, and to some extent certain sense organs. Some information has come to light concerning all of these systems, possibly excepting the urogenital system.

Patten (1904, p. 116; 1912, pp. 369–372) recognized that the differential sedimentation seen in sections of *Bothriolepis* was "produced by some organic structure(s)," but his interpretations of these structures are for the most part incorrect. Moreover, he fails to put forward any hypothesis as to the method by which the form of the organs was preserved.

Alimentary system.—The alimentary tract is relatively simple and straight. The small mouth cavity is clearest in D.C.M.[1] 12632 where it is seen as a pocket over the posterior part of the mental ("upper jaw") plates (figs. 1A, 6). Directly posterior to the mouth region the alimentary tract becomes wide and dorsoventrally flattened.

[1] Darmouth College Museum.

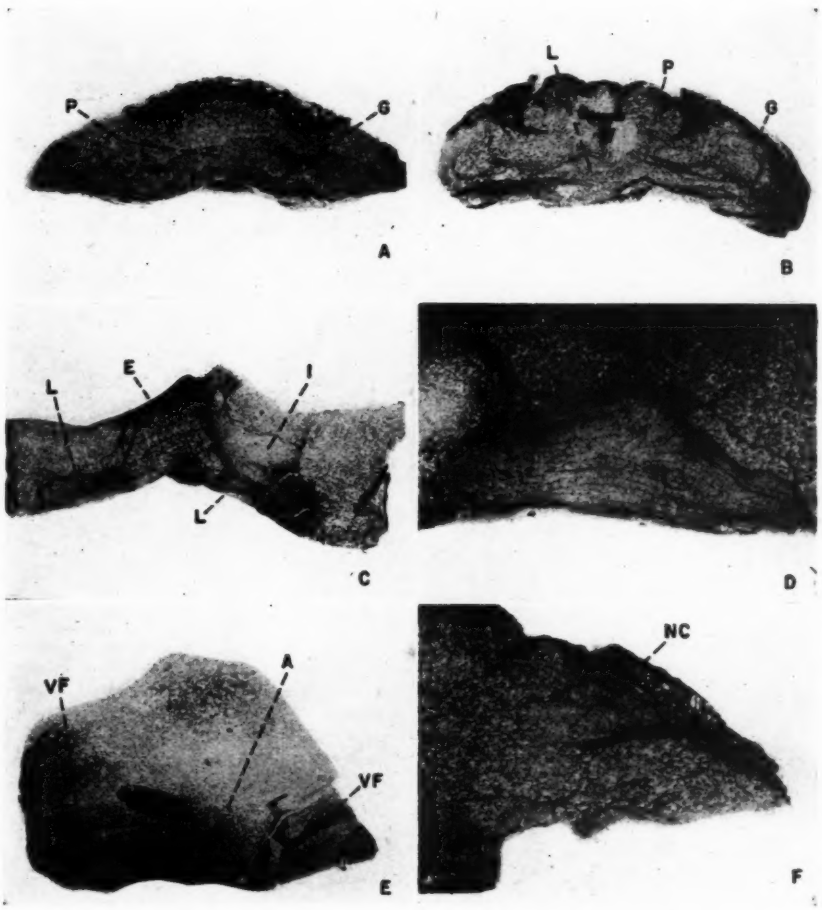

FIG. 1—Sections of *Bothriolepis canadensis* Whiteaves. *A*, Transverse section through anterior head region of D.C.M. 12632 showing gill passages leading from pharynx region. *B*, Transverse section through orbital region of D.C.M. 12640, ×5/4, showing coiled structures interpreted as gills. *C*, Transverse section through trunk region of D.C.M. 12640, ×1, showing paired lungs and intestine. *D*, Transverse section through intestine of D.C.M. 12632, ×2, showing spiral structure. *E*, Transverse section through anal region of D.C.M. 12641. *F*, Sagittal section through head of D.C.M. 12638, ×3, showing nasal capsules.
A, Anus; E, esophagus; G, gills; I, intestine; L, lungs; NC, nasal capsule; P, pharynx; VF, ventral "frill."

From this region arise both gills and lungs, thus it may be called the pharynx. The esophagus is less satisfactorily preserved, due perhaps to the fact that the sediment could not penetrate easily so far. Parts of it are distinguishable in all of the sections selected for study, while its whole length may be traced in D.C.M. 12640. It appears to be a very wide, dorsoventrally flattened tube, although crushing of the specimens may have exaggerated the flatness considerably. Posteriorly it often contains carbonaceous material, which was described by Patten (1912, pp. 379–380) as the remains of plant material which "represents the contents of the stomach." In this he is undoubtedly correct, although the stomach region of the alimentary canal cannot be distinguished by any expansion such as is present in most living fish. The esopha-

gus and stomach appear to lead into the flattened ellipsoidal structure which may be homologized with the anterior intestine of other fish. This intestine is present in all of the sections examined and is invariably filled with the fine silt or mud described above, which the animal undoubtedly ingested while alive. In some specimens the intestine is small; in others it is so expanded with mud that it nearly fills the trunk carapace. The anterior end of the intestine, which is not far posterior to the articulation between the head and trunk, is narrow; then it expands transversely rapidly (fig. 4). Its dorsoventral dimension is not so great, though this may be due in part to crushing. It narrows abruptly posteriorly and leads into the short rectum.

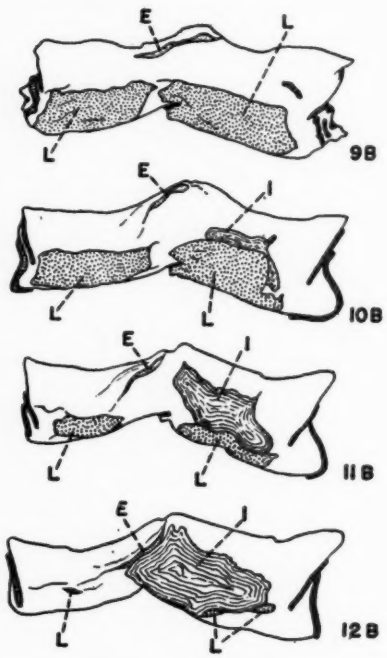

FIG. 2—Transverse serial sections through the anterior trunk region of D.C.M. 12640. E, Esophagus and "stomach"; I, spiral intestine; L, lungs.

In sections the intestine shows numerous more or less concentric dark lines (fig. 1D). These are difficult to trace in detail, but in a few of the best preserved transverse sections the lines have a definite spiral rather than concentric arrangement (fig. 3A), thus it is probable that this intestine contains a rather complex spiral valve comparable to that in elasmobranchs and many bony fish. This is confirmed by the manner in which the anterior alimentary tract leads into the intestine (fig. 2); instead of meeting the intestine terminally, it comes to lie on its left dorsal side. In some sections (D.C.M. 12637, 12638, 12640), the relatively coarser matrix of the esophagus may be traced into the exterior spiral of the stomach (fig. 3B),

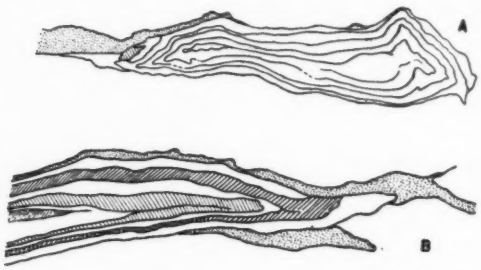

FIG. 3—*A*, Transverse section through the intestine of D.C.M. 12641 to show the spiral structure. *B*, Sagittal section through the spiral intestine of D.C.M. 12638 showing the anterior alimentary tract (stippled) entering the outer spiral.

and in D.C.M. 12644 it fills the exterior spiral for nearly the whole length of the intestine (fig. 4).

As interpreted from various sections, the spiral valve is of the "scroll type," found among elasmobranchs in the Carcharinidae and Sphyrnidae. In this type, the valve is formed by a single fold of tissue rolled into a scroll upon its own axis, parallel to the axis of the intestine. It may be compared very closely to that of *Sphyrna zygaena*. In transverse sections through the center of the spiral valve there may be counted 12 to 14 distinct layers, indicating that there are six or seven complete spirals.

The spiral intestine tapers rapidly posteriorly to lead into a short, cylindrical rectum (figs. 5, 8) which lacks the spiral structure. It terminates above the disclike anal plate which lies just within the posterior end of the trunk carapace.

Gills.—Patten (1904, pp. 123–124; 1912, pp. 367–368, 371) concluded that the gills could not have been in the head for the reason that the "extra-lateral" (i.e., oper-

cular) plate is the only plate which could function as an operculum, and that its movement is too restricted. On the contrary, he identified as gills the "laminated organ" which has been described in this paper as the intestine. He further believed that water passed from the "laminated organ" into an atrial chamber and made its exit at the posterior end of the "branchiocephalon" (i.e., trunk carapace).

Against this theory the following objections may be brought: (1) *Bothriolepis* has been shown to be a true, if aberrant, gnathostome (Stensiö, 1931, pp. 158–160), while such an arrangement as he postulates is not conformable with the gnathostome plan. (2) The "laminated organ" is shown definitely to be part of the alimentary system by its connection with that part of the esophagus which often contains carbonized material (i.e., the stomach), and by the fact that posteriorly it leads into the median, unpaired tube, terminating at the anal plate, which could hardly be other than the rectum. (3)

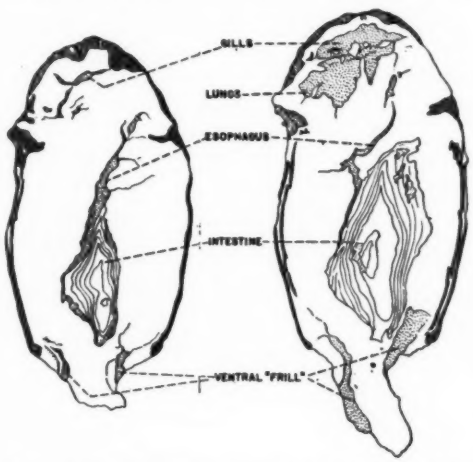

FIG. 4—Horizontal sections through D.C.M. 12644.

As Stensiö's researches have shown (1931, p. 58), the extralateral or opercular plate is not rigidly attached to the surrounding plates but has its posteroventral margins free and could be dilated. (4) There is no evidence for the presence of an atrial chamber.

As Stensiö concluded, the gills were undoubtedly in the region covered by the head shield, and traces of structures may be seen in sections of some of the best-preserved specimens which are identified as gills (figs. 6, 7). D.C.M. 12632 (fig. 1A) shows ducts extending laterally from each side of the mouth and pharynx region. In D.C.M. 12640 these ducts are seen to extend into curled structures lying against the side and

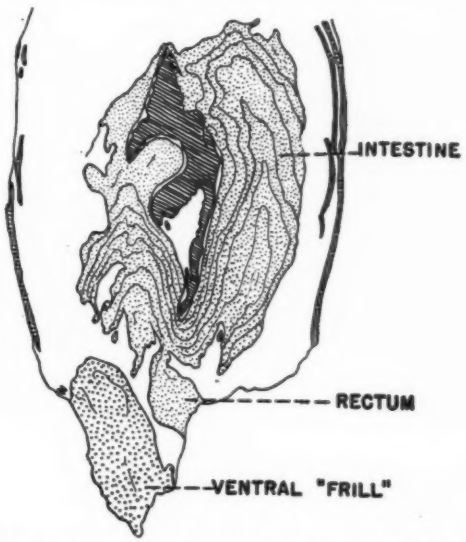

FIG. 5—Horizontal section through D.C.M. 12644.

top of the head shield (fig. 1B). At their most complete development these curled structures might be described as unclosed rings. An attempt was made to determine the exit of these gills. Some sections show a lateral projection or continuation of the curled structures extending toward the opercular region. But the preservation is so incomplete that as strong a case might be made from this evidence for a gill exit between the opercular and sufflaminal plates as for one below the opercular plate.

Any interpretation of the structure of the gills is certain to be unsatisfactory and inconclusive from the evidence available. Thick sections were used for study, thus much needed detail is missing, and in only one specimen is the structure preserved with what may be regarded as any completeness. The following generalizations may be made, however: Between the pharynx and gills are passageways or ducts leading to the gills.

The curled structures may represent a section through two gill pouches, whose direction is at an angle to the plane of the transverse sections. The coarse matrix in the center of the curled structures represents the interbranchial septa, whose space was filled at a later time. The fact that the curled structures are closed laterally signifies

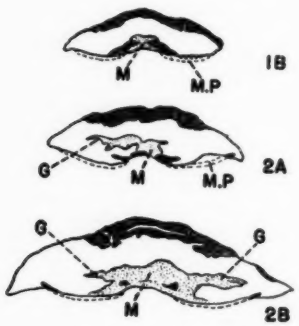

FIG. 6—Series of transverse sections through the anterior head region of D.C.M. 12632. G, Gills; M, mouth region; MP, mental plates.

that the gill pouches lead into a common extrabranchial chamber and have a common opening either below or above the opercular plate.

In summary, it may be said that there can be little doubt that the gills are located in the head. The position of the gill chamber is fairly well defined by the sections described and by the structure of the interior of the head shield. The gill chamber extends to the dermal cranial roof and lies dorsally against the concave inner surfaces of the lateral parts of the lateral and lateral nuchal plates, and laterally against the whole inner surface of the sufflaminal and perhaps the opercular plates. Posteriorly it is bounded by the crista transversalis interna anterior of the anteroventrolateral plates. The neurocranium lies against the medial part of the dermal cranial roof, and its probable boundaries are marked by a sharp projection on the inside of the lateral and lateral nuchal plates. It is probable that the gill chambers extend medially somewhat under the neurocranium. Compared to a fish of more normal shape, it may be said that the gill region is relatively short and broad, more dorsally placed, and crowded more anteriorly.

It is possible that a more completely preserved specimen will demonstrate the presence of a prehyoidean gill slit such as Watson (1937) has demonstrated in acanthodians. At present there is no direct evidence on the number of gill slits.

Lungs.—In the sections selected for study there may be seen paired ventral sacs, which extend posteriorly into the trunk carapace about as far or a little farther than the anterior end of the spiral intestine (figs. 1C, 2). In D.C.M. 12640 these sacs appear to arise anteriorly from the ventral surface of the pharynx as a single median tube, which broadens rapidly and separates into two sacs shortly posterior to the orbital region (fig. 7). The other sections are not as clear anteriorly, but all indicate a connection with the alimentary tract in the pharynx region. The spiral intestine often rests on the posterior end of the right sac, but there is no evidence of any open connection between the two, and in some specimens the right sac ends anterior to the spiral intestine.

These sacs have the same position and relationships as the lungs of certain dipnoans and tetrapods, and this is the most acceptable interpretation of them, if the assumption is credited that they represent fillings by sediments of organs that communicate with the exterior. Since there is no evidence

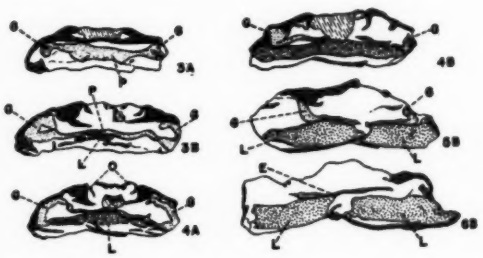

FIG. 7—Transverse serial sections through the head and anterior trunk region of D.C.M. 12640. E, Esophagus; G, gills; L, lungs; O, orbits; P, pharynx.

of any communication between the external nasal passages and the mouth region, it is probable that *Bothriolepis* gulped air in the same manner as do the present-day lung fishes.

That this Upper Devonian fish should possess lungs as well as gills is not as re-

markable as it might seem at first sight. It is known that Amphibia had appeared by Upper Devonian times and presumably possessed functional lungs derived from those of their crossopterygian ancestors. Two crossopterygians, *Eusthenopteron* and *Holoptychius* are found in the same beds as *Bothriolepis*. The "lung-fish" or dipnoan, *Scaumenacia*, is another element in the same faunule, and it is very possible that it had already developed lungs, since the group has been so conservative in other points in its evolution since Upper Devonian times. Finally, the geological sequence indicates fluviatile conditions in a period of mountain building. These are precisely the conditions under which could occur occasional droughts, and presumably those under which lungs originated.

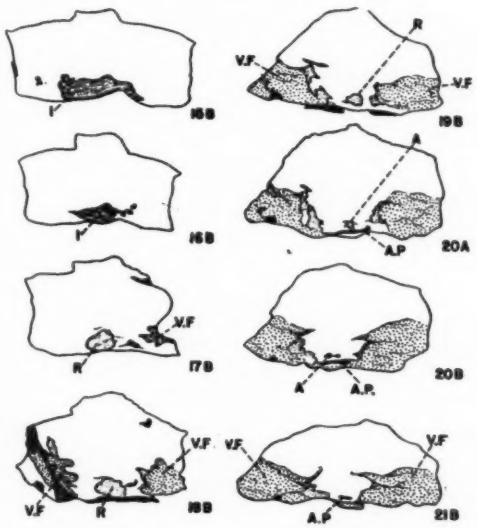

FIG. 8—Transverse serial sections through the posterior trunk region of D.C.M. 12641. A, Anal region; AP, anal plate; I, intestine; R, rectum; VF, ventral "frill."

It might be hoped that *Bothriolepis*, since it has the earliest known lungs, would furnish evidence on the manner in which lungs originated, whether as independent esophageal diverticula or as modified gill pouches. All that can be said, however, is that there is no evidence in *Bothriolepis* of serial homology between the lungs and gills. Moreover, if such a homology existed, it is possible that it was already masked by specializations correlated with the shortness and breadth of the head.

Ventral "frills."—At the posterior end of the trunk carapace on either side of the tail may be seen in some well-preserved specimens of *Bothriolepis* the projecting processes described by Patten (1912, p. 371) as the

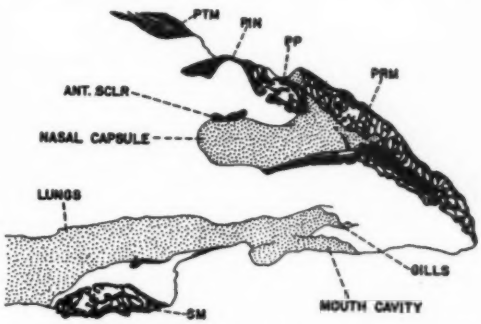

FIG. 9—Sagittal section through the head of D.C.M. 12638. ANT. SCLR., Anterior sclerotic plate; PIN, pineal plate; PP, prepineal plate; PRM, premedian plate; PTM, postmedian plate; SM, semilunar plate.

"atrial frill." They show clearly in sections and may even be exposed by dissection due to their contrasting sediment.

No entirely satisfactory theory has been proposed to account for these organs. Patten considered them to be frills around the atrial opening, but since there is no evidence that there was an atrial cavity in the trunk carapace, this theory cannot explain their function. Stensiö (1931, p. 138) states that "this frill . . . obviously had such a position that it is very likely that it represents the ventral fins." But if one accepts the theory stated earlier in this paper that the preservation of the form of these organs is due to the filling of a cavity having open communication with the exterior, Stensiö's statement is not as easy to accept, for fins, in the strict sense, are not hollow organs. Of course, a fin, if curled up, would form a basin which could catch and hold sediment, and this may be a partial explanation of the ventral "frills."

But the explanation is not so simple as this, for sections show that the ventral "frills" have two distinct elements (figs. 1E, 8) separated by sharp boundaries and

distinguished by their two different sediments. The lateral element makes up most of the paired "frills," and it is this part which is seen in dissections, from which Patten has made his restoration (1904, fig. 1). Sections show that this lateral part of the ventral "frill" is made up of the same fine-textured sediment that fills the gills, lungs,

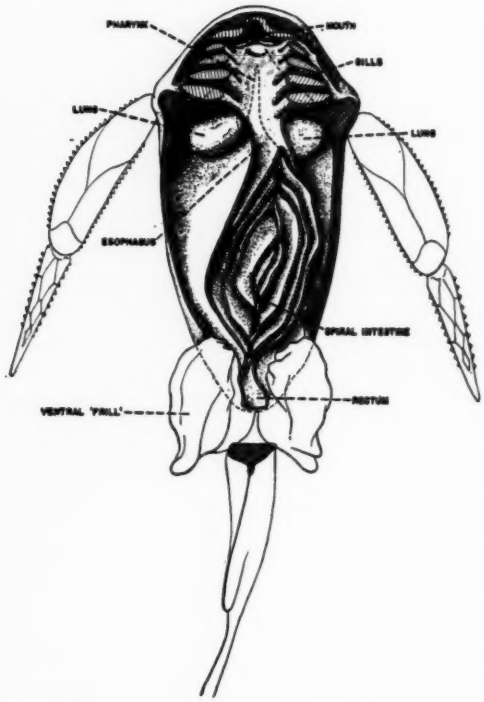

FIG. *10*—Attempted restoration, ×½±, of some of the soft anatomy of *Bothriolepis*, shown as a dorsal view of a horizontal section.

and anterior alimentary system. It may show a definite structure, marked by distinct lines, which can be interpreted as an incurling or an infolding of the lateral part of the "frill." This part of the "frill" is clearly demarcated, except sometimes dorsally, where there may be an intergrading into the coarser sediment surrounding the animal and filling much of its interior. This may be taken to indicate that the opening through which the filling took place was dorsal.

There is little evidence for a satisfactory interpretation of this part of the "frill." If it represents a fin, the fin was not of the usual type found in fishes, but must have been a relatively soft, flexible appendage, which was or could be curled or infolded. There is no evidence of any skeletal support, but some unossified support may have been present. It is possible that these organs represent some reproductive organ, such as a clasper similar to that in elasmobranchs, or a brood pouch. A census of 38 exceptionally well preserved specimens which show the tail clearly shows no frill in a little less than half. This suggests that these organs were present in one sex and not in the other, but it is in no way conclusive, since the preparation of many individual specimens is incomplete.

On the median side of the lateral parts of the ventral "frill" are distinct structures, visible in transverse sections and usually distinguished by differences in the filling sediment. This sediment has the appearance of a mixture of the extremely fine material found in the intestine and the medium material of the lateral part of the "frill," although sometimes it is more purely one or the other. These organs take the form of an irregular crescent applied to the median side of the lateral part of the "frill," and show points or processes projecting laterally and medially. One of the median processes extends to or toward the dorsal surface of the rectum, but in no case has there been found any open connection with the alimentary system. It is possible that there was a cloaca into which both these organs and the rectum opened, and there is a suggestion in one or two cases that this may be the case. If this is so, these organs might be interpreted as some urogenital sinuses, bladders, or ducts.

Nasal capsules.—Of interest is D.C.M. 12638, in which the medium-textured sediment preserves the form of what is apparently the nasal capsules (figs. 1F, 9). The capsules occupy the space above the shelf formed by the lamina suborbitalis of the premedian and lateral plates, and extend posteriorly under the orbits. They communicate with the exterior near the median line and anterior to the pineal and prepineal plates.

This discovery confirms Patten's belief (1904, p. 122) that the external nasal apertures lay on the dorsal side of the head, in

the deep emargination on each side of the prepineal plate. Since the capsules extend well under the eyes, Patten is probably correct in stating that the peculiar emargination on the medial side of the most anterior part of the sclerotic ring was the lateral boundary of the external nasal aperture of its side. It could not form the posterolateral wall of the nasal capsule, as Stensiö believed (1931, p. 57).

Furthermore, these specimens furnish evidence that the ethmoidal region of the endocranium was short and lodged in the space dorsal to the lamina suborbitalis. Stensiö (1931, p. 54) inferred this from the absence of a supraorbital sensory canal on the preorbital part of the dermal cranial roof and from the position of the external nasal apertures. He believed, however, that the orbital cavity had its anterior wall formed by the posterior wall of the olfactory capsule. Since the nasal capsules extend well under the orbits, it seems probable that there has been some telescoping of the olfactory and orbital regions of the endocranium, and that the latter has come to overlie the former to some extent. This may be correlated with the relative shortness of the head.

SUMMARY

1. The form of certain internal and external organs of *Bothriolepis* is preserved as fillings by easily distinguishable sediments.

2. The alimentary system is primitive in being a straight, uncoiled tube, without an expanded stomach region, but is specialized in having a complex spiral valve, comparable to that in certain families of sharks. This is not necessarily indicative of a close relationship to sharks, as it was more probably independently acquired.

3. Inferentially the gills were of a primitive type, but little can be told of their structure. They occupy much of the space under the lateral part of the head shield, are placed well anteriorly, and are covered by an opercular fold laterally.

4. Paired ventral lungs are present. As lungs were acquired by several groups of fresh water fish, probably in the Devonian as a response to climatic conditions, this is not a unique case.

5. Paired urogenital sinuses or ducts are possibly represented lateral to the rectum. The ventral "frills" proper may be soft fins or some reproductive organs.

6. The preservation of nasal capsules just under and anterior to the orbits is interesting, since it definitely establishes the position of the external nasal openings and of the anterior end of the neurocranium.

REFERENCES

PATTEN, WILLIAM, *1904*, New facts concerning *Bothriolepis: Biol. Bull.*, vol. 7, no. 2, pp. 113–124.

——, *1912*, *The evolution of the vertebrates and their kin*. Blakiston's, Philadelphia.

STENSIÖ, ERIK, *1931*, Upper Devonian vertebrates from East Greenland: *Meddelelser om Grønland*, Band 86, Nr. 1.

WATSON, D. M. S., *1937*, The acanthodian fishes: *Royal Soc. London, Philos. Trans.*, ser. B, vol. 228, pp. 49–146.

MANUSCRIPT RECEIVED BY THE EDITOR FEBRUARY 27, 1941.

JOURNAL OF PALEONTOLOGY, VOL. 15, NO. 5, PP. 562–563, 1 TEXT FIG., SEPTEMBER, 1941

AN ANAPTOMORPHID PRIMATE FROM THE OLIGOCENE OF MONTANA

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DURING the field seasons of 1937, 1938, and 1939, Carnegie Museum field parties under the direction of Mr. J. LeRoy Kay have been engaged in stratigraphic studies of the Tertiary formations of southwestern Montana. The fossil mammals of Montana will form the subject of an exhaustive study during the next few years. One specimen collected by the 1939 expedition is, however, of sufficient general interest to warrant publication in advance of the main collection, and the Museum takes this opportunity to do so. Mr. Sidney Prentice made the drawing for this paper.

Family ANAPTOMORPHIDAE
Subfamily OMOMYINAE
MACROTARSIUS MONTANUS
Clark, n. gen., n. sp.
Text figure 1

Type.—Partial right ramus mandibuli, bearing P_4, M_{1-3} complete, partial C and P_3, alveoli of I_{1-2}, P_2, Carnegie Museum number 9592.

Horizon.—Chadron.

Locality.—North face of the range, 1½ miles southeast of Cold Springs, North Boulder valley, Jefferson County, Montana.

Generic and specific characters.—Dental formula ?/2-1-3-3. I_1 enlarged, I_2 extremely reduced. Canine reduced, apparently less prominent than in the other genera of the Omomyinae. P_3 with a posteroexternal cuspule. P_4 submolariform, with both paraconid and metaconid, and a short, transversely basined heel. Molar paraconids distinct from metaconids, connected with protoconids by a prominent crest. Molar paraconids all internal rather than submedian. Molar series one-third longer than all others combined. A definite hypoconulid on M_1 and M_2. Hypoconulid of M_3 simple, basined, but very long, with a sharply angulated constriction separating it from the rest of the tooth. Three mental foramina, directed upward, with the anterior foramen notably the largest.

Measurements.—Tooth row, I_1–M_3, measured along alveoli, 25 mm.; M_1–M_3, 15 mm.; P_4, anteroposteriorly, 3.4 mm.; P_4, transversely, 3.4 mm.; M_1, anteroposteriorly, 4.5 mm.; M_1, transversely, across hypoconid and entoconid, 4.2 mm.; M_2, anteroposteriorly, 4.6 mm.; M_2, transversely, across hypoconid and entoconid, 4.1 mm.; M_3, anteroposteriorly, 6.0 mm.; M_3, transversely, across hypoconid and entoconid, 3.6 mm.

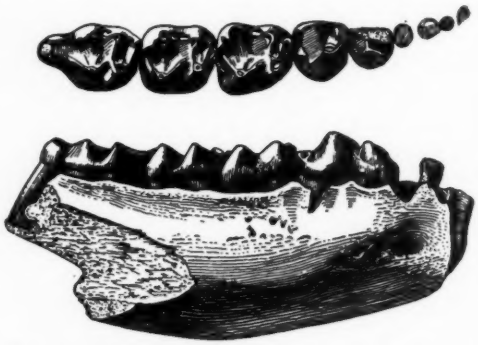

FIG. 1—*Macrotarsius montanus* Clark, n. sp., type, external and crown views, ×2½.

Discussion.—Under Wortman's (1904) original definition of the Omomyinae as a subfamily of the Anaptomorphidae, characterized by nine teeth in the lower jaw, *Macrotarsius montanus* is clearly a member of that subfamily. *Macrotarsius* is a member of the Omomyinae under Simpson's revised diagnosis of the subfamily, also.[1]

Several of the distinguishing characters of *Macrotarsius montanus* are developments of tendencies already existent in the better-known Bridger genera of the subfamily. Reduction of the canine, increase in size of the molar series proportionally to the rest of the

[1] The revised diagnosis occurs in a study of North American primates, not yet published, which Dr. Simpson has very kindly permitted me to use.

teeth, reduction of I_2, molarization of P_4, and general increase in size, might have been predicted for an omomyine occurring so late in time.

Many of the characters of *Macrotarsius*, however, have not such obvious antecedents in the Bridger forms. The molar paraconids, though completely separate from the metaconids, are joined to the protoconids by strong crests. Furthermore, the paraconids are all lateral rather than submedian. In the Eocene genera each molar expands posteriorly, while M_2 and M_3 of *Macrotarsius* do not expand, and M_1 retains but a little posterior swelling. Also, the long, simple, anteriorly constricted hypoconulid of M_3 has no parallel in the earlier forms. A low flange occupies the median portion of the posterior border of M_1 and M_2, in the position of the hypoconulid. However, it is more a posteriorly directed crest than a true cusp. The mental foramina are large and three in number rather than two as in the other genera.

The large symphyseal area, with doubly convex borders, extends back to a point beneath the anterior portion of P_3. A deep pit immediately behind the posteroventral end of the symphyseal area leads into a fossa, which passes forward across the symphyseal surface, parallel to its ventral border, almost to the alveolus of the first incisor. Otherwise, the jaw fragment preserved posesses no characters worthy of note.

Comparison with the two known Sespe genera, *Dyseolemur* (Stock, 1934) and *Chumashius* (Stock, 1933) reveals that, unfortunately, *Macrotarsius* has probably no direct genetic relationship with either.

Wrinkled enamel, presence of metastylids, median position of the molar paraconids, and very much reduced M_3 may all be regarded as specializations in *Dyseolemur* (although some of these characters occur in *Washakius* also). None of them occur in *Macrotarsius*.

Although *Macrotarsius* is somewhat closer, probably, to *Chumashius* than to *Dyseolemur*, quite apparently it was not derived from *Chumashius*. Reduction of the molar paraconids has progressed farther in the latter than in *Macrotarsius;* the median position of the paraconids in *Chumashius* is also a specialization more advanced than the condition in *Macrotarsius*. Whether the presence of a metaconid on P_4 is primitive or advanced, I do not know: Stock (1933, p. 957) considers it primitive, and if so *Chumashius* is much more advanced than *Macrotarsius*, in which the metaconid is prominent.

Macrotarsius resembles *Hemiacodon* more closely than it does the other described genera of the subfamily. However, the characters listed differentiate it from *Hemiacodon* so sharply as to leave little doubt of its generic identity. It resembles the living *Tarsius* even less, notably through its reduced canine and molariform fourth premolar, than do some Eocene genera of the Omomyinae. The fragmentary type indicates only that *Macrotarsius montanus* is probably more closely related to *Hemiacodon* than to any other known genus, and very probably is not ancestral to any living primates. Its presence in the lower Oligocene of southwestern Montana might lead to hypotheses regarding the climate and vegetation of its environment. However, it seems best to avoid such speculation until studies of the entire lower Oligocene fauna of the area are complete.

REFERENCES

STOCK, CHESTER, *1933*, An Eocene primate from California: *Nat. Acad. Sci., Proc.*, vol. 19, pp. 954–959.

——, *1934*, A second Eocene primate from California: *idem*, vol. 20, no. 2, pp. 150–154.

WORTMAN, J. L., *1904*, Studies of Eocene Mammalia in the Marsh Collection. Peabody Museum: *Am. Jour. Sci.*, ser. 4, vol. 17, p. 29.

MANUSCRIPT RECEIVED BY THE EDITOR APRIL 15, 1941.

JOURNAL OF PALEONTOLOGY, VOL. 15, NO. 5, P. 564, 1 TEXT FIG., SEPTEMBER, 1941

BALTIC ORDOVICIAN FAUNA IN GASPÉ

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ABSTRACT—The appearance of the bryozoan species *Hallopora tolli* Bassler in eastern Gaspé is important in that it not only emphasizes the great extent of the Middle Ordovician seas in North America but it also serves to corroborate the current opinion that the advance of these marine waters was from the north.

THE DISCOVERY of the Baltic species *Hallopora tolli* Bassler (1911) in Gaspé is of considerable significance. As far as I am aware, no Ordovician fauna has been reported up to the present time from that part of the continent. The figured specimen

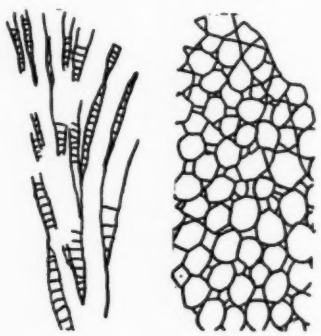

FIG. 1—*Hallopora tolli* Bassler. Vertical and tangential sections, ×10.

(Royal Ontario Mus. Palaeontology plesiotype 23355) was found with others in Joncas township, Gaspé county, in the southeastern part of the Gaspé peninsula. The locality is rather inaccessible, being situated between the headwaters of the Little Pabos river and the west fork of the Grand river.

H. W. McGerrigle (1940) of the Quebec Bureau of Mines, who kindly sent me his collection for study, considered these rocks, from his field studies, to be of Ordovician age and included them in the White Head formation. The more exact time relationships, however, were not determined until this palaeontological evidence became known.

Hallopora tolli was originally described from rocks of supposed Black River age in Esthonia. Bassler has reported that 35 per cent of the bryozoan species in this Baltic province and North America are alike. Evidence points to the fact that the Russian species entered this continent from the north, since Baltic species are known to occur in several localities in the northern part of North America including Baffin Land and Lake Nipissing, Ontario.

The particular species under discussion has not hitherto been mentioned among the faunas of this continent. A specifically different, though very closely allied form, *Hallopora perampla* (Ulrich and Bassler) has been reported by Bassler in the lowermost Trenton strata at Belleville, Ontario. It differs in having much larger zooecia, which, as the surface is approached, pinch out the mesopores.

The finding of *Hallopora tolli* at this far eastern point in Canada is added proof of the great spread of the Middle Ordovician sea and substantiates the belief that the direction of advance of these waters was from the north.

REFERENCES

BASSLER, R. S., *1911, U. S. Nat. Mus., Bull.* 77, p. 333, text fig. 209.

MCGERRIGLE, H. W., *1940*, Advance report on the Power-Joncas area, Gaspé County: *Quebec Bur. Mines Prelim. Report* 153.

MANUSCRIPT RECEIVED BY THE EDITOR MAY 23, 1941.

JOURNAL OF PALEONTOLOGY, VOL. 15, NO. 5, PP. 565–566, SEPTEMBER, 1941

FENESTELLA LONSDALE AND FENESTRELLINA D'ORBIGNY

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THIS IS a notice to all naturalists concerned that we appeal to the International Commission on Zoological Nomenclature for suspension of the Rules of Zoological Nomenclature in the case of *Fenestella* Lonsdale, the well-known genus of late Paleozoic cryptostomatous bryozoans, and for retention of this name as a *nomen conservandum.*

Although Bassler acted correctly in accord with the Rules when, in 1935, he rejected *Fenestella* Lonsdale as homonym of *Fenestella* Bolten, we find in our study of the late Paleozoic fenestrate bryozoans that the name *Fenestrellina* d'Orbigny, recommended by Bassler to take the place of *Fenestella*, is inacceptable because it is based on species not congeneric with *Fenestella* Lonsdale.

Because of the situation that confronts us we are forced to follow one of the two courses open to us; to select, in strict application of the Rules, another name in place of the homonym *Fenestella* Lonsdale, or to apply to the Commission for the retention of *Fenestella* Lonsdale as a *nomen conservandum.* We choose the latter course because it appears that the other course would result in greater confusion than uniformity. Pending the decision of the Commission on this taxonomic case we propose to continue the use of *Fenestella* Lonsdale in our work, reserving *Fenestrellina* d'Orbigny for fenestrate bryozoans not congeneric with *Fenestella* and combining characters of *Fenestella* and *Thamniscus.*

Following is a brief outline of the points in the case, divided into enumerated paragraphs for convenience of reference by those who are interested in the problem.

TAXONOMIC PROBLEM OF FENESTELLA—FENESTRELLINA

1. The name *Fenestella* was originally, in 1798, applied to a pelecypod, but in 1839 Lonsdale employed it for a group of the late Paleozoic cryptostomatous bryozoans, and it has since been widely used in this latter sense.

2. In 1935 Bassler suspended the name *Fenestella* for the bryozoans in accordance with the strict application of the International Rules of Zoological Nomenclature. In place of *Fenestella* Lonsdale, Bassler substituted the name *Fenestrellina* d'Orbigny. However, the genotype of *Fenestrellina* is *F. crassa* McCoy (designated by d'Orbigny in 1844), a *Thamniscus*-like form, whereas the accepted genotype of Lonsdale's *Fenestella* is *F. plebeia* McCoy, 1844, a species with short and regular fenestrules.

3. In 1881 Shrubsole, the only author to re-examine topotypes (if not the type) of McCoy's *F. crassa*, pointed out that this species does not belong to the genus *Fenestella*, but "to another fenestrate genus of Polyzoa."

4. In our opinion, based on an analysis of the illustrations and descriptions by McCoy and Shrubsole, *F. crassa*, together with at least three more known Lower Carboniferous species none of which has been found in America, constitute a compact group, which deserves to be separated into a distinct genus, which would have the same morphologic relation to *Fenestella* Lonsdale as *Thamniscus* King has to *Polypora* McCoy.

5. Acceptance of *Fenestrellina* d'Orbigny as a genus separate from *Fenestella* Lonsdale brings the taxonomic status of the latter back to where Bassler found it in 1935. A possible solution of the problem, in accord with the strict application of the Rules, would be to give *Fenestella* Lonsdale still another name. Our only other way to solve the problem is to request the International Commission on Zoological Nomenclature to suspend the Rules for this case and to preserve *Fenestella* for this bryozoan genus as a *nomen conservandum.*

6. The reasons for preserving the name *Fenestella* are as follows:

a, The name *Fenestella* for late Paleozoic bryozoans has been and still is widely used in American and foreign textbooks on paleontology and historical geology,

and no other name for the same fossil bryozoans is used generally.

b, The generic name *Fenestella* for a living lamellibranch was erected in an obsolete publication by Bolten (1798) and since has been corrected in transcription (but not in the meaning) to *Fenestrella* by Gray (1847) and, besides, was placed in synonymy of the well known genus *Anomia*. Therefore, even if an attempt should be made to restore the name *Fenestrella* as a subgeneric or generic name for a part of the lamellibranchs usually placed in *Anomia*, the name *Fenestella* could not be used for it again. Therefore, no confusion can arise if the name *Fenestella* be retained for the genus of late Paleozoic cryptostomatous bryozoans.

c, The name *Fenestella* for these bryozoans is still in use in the extensive Russian literature on the late Paleozoic bryozoans, and the Russian bryozoologists have refused to substitute the name *Fenestrellina* for *Fenestella*. In America few authors publishing papers since 1936 have substituted the name *Fenestrellina* for *Fenestella*.

CONCLUSION

In view of the situation as herein outlined, it seems that suspension of the Rules in the case and the restoration of the name *Fenestella* for the late Paleozoic cryptostomatous bryozoans would cause much less confusion than to continue the usage of *Fenestrellina* in the broad sense, as suggested by Bassler, or to accept still another name for Lonsdale's genus in the restricted sense.

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JOURNAL OF PALEONTOLOGY, VOL. 15, NO. 5, P. 566, SEPTEMBER, 1941

A SPARGANIUM FROM THE UPPER CRETACEOUS OF WYOMING

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IN 1874 Heer[1] described a plant of the family Sparganiaceae from the early Upper Cretaceous of western Greenland and named it *Sparganium cretaceum*. Among fossil plants collected along the east flank of the Wind River Range about 15 miles north of Dubois, Wyoming, were found several specimens that have been identified as this species. Although there is little in the way of specific characters in any of the older *Sparganium* fruits, these specimens were identified as such because of their close resemblance to the figures of that species, which is the only *Sparganium* described from the early Upper Cretaceous rocks.

The rather numerous and well-preserved fruit heads and stem fragments were interbedded with several species of leaves of early Cretaceous age. They resemble very closely *Sparganium stygium* Heer,[2] which species, however, has never been described from rocks as old as this.

The writer believes that this is the first reported discovery of *Sparganium cretaceum* in the Cretaceous rocks of Wyoming. She is greatly indebted to Prof. E. W. Berry[3] of Johns Hopkins University for his invaluable assistance in the identification of this species.

[1] HEER, OSWALD, *1874, Flora fossilis arctica*, vol. 3, p. 105, pl. 28, f. 12.

[2] HEER, OSWALD, *1855, Flora Tertiaria Helvetiae*, vol. 1, p. 101, pl. 14, f. 1–4.

[3] Written communication.

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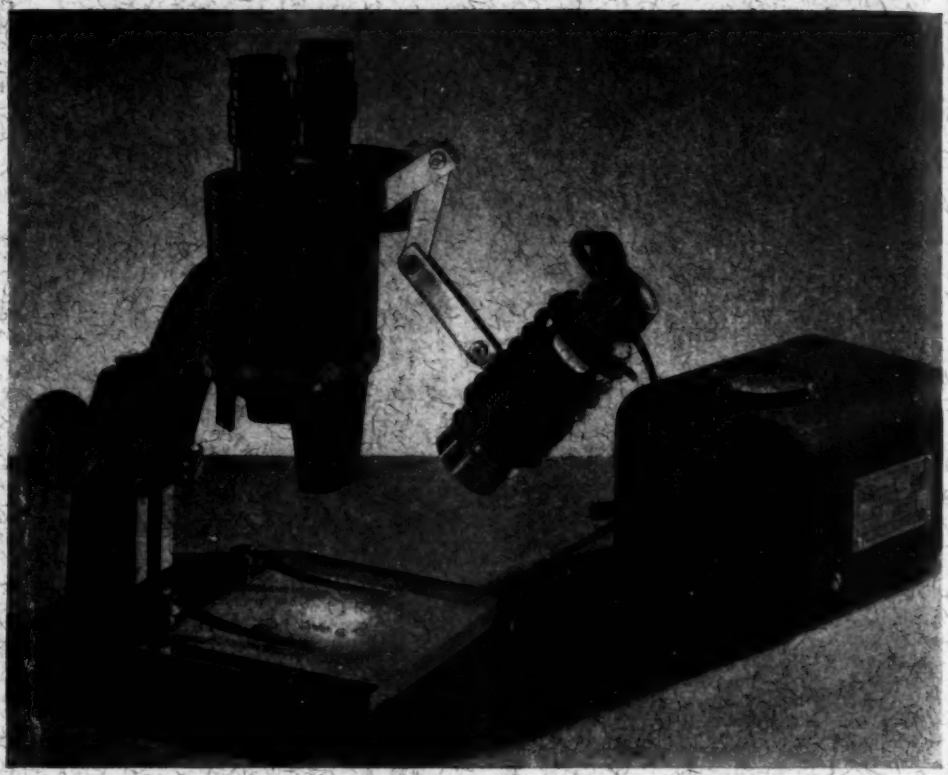

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